Chapter 7

Micromorphology of Soil Organic Matter*

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DEDICATION

I dedicate this work in gratitude to the memory of Prof. Dr. h. c. Dr. W. Kubiena.

I wish to express my thanks to some colleagues for their critical reading of the manuscript. Among them I am particularly indebted to Dr. G. Zachariae, then Freiburg i. Br., who has given me many valuable hints, especially concerning the sections which touch on zoological problems. My thanks are also due to Dr. N. Walker, Rothamsted, for the translation of the manuscript into English.

Contents

	page
I. *Introduction*	371
A. Fundamentals of humus micromorphology	371
B. Applicability of humus micromorphology	373
II. *Survey of the microscopic structure of humus formations*	374
A. The constituents	375
1. Plant residues	375
2. Organic fine substance	375
3. Mineral constituents	377
B. The fabric	377
C. The profile	377
III. *The organic constituents of humus soil horizons*	379
A. Animal residues	379
B. Plant organ and tissue residues	380
1. Parent material	381
2. Decomposition of tissues	385
a) General phenomena	385

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b) Parenchymatous tissues 386
α Morphology 386
β Microbiology 390
γ Chemistry 390
c) Phlobaphene-containing tissues 391
α Morphology 391
β Microbiology 393
γ Chemistry 395
d) Lignified tissues 396
α Morphology 396
β Histochemical and histophysical investigations 399
γ Microbiology 400
δ Chemistry 401
e) Other tissues 401
C. Organic fine substance 403
1. Mechanical disintegration of the plant residues 404
a) Disintegration by the activity of animals 404
b) Disintegration by other processes 406
2. The constituents of the fine substance 406
a) Morphologically identifiable tissue residues 406
b) Morphologically fully destroyed material 407
c) Microorganisms and their residues; pollen 410
d) Opaque particles 412
e) Particles from the solution phase 413
3. The chemistry of the fine substance 414
D. Organic matter in the mineral soil 416
1. Blending of the organic matter into the mineral soil 416
2. Holorganic constituents in the mineral soil 417
a) Plant residues 417
b) Organic fine substance 417
3. Organic matter as pigment of the mineral fine substance 419
IV. *Fabrics in humus soil horizons* 420
A. Processes of fabric formation and stabilization 420
1. Nonbiological processes 420
2. Fabric formation by roots and microorganisms 421
3. Fabric formation by animals; droppings 422
B. Fabric types in humus soil horizons 428
1. Fabrics with plant residues prevailing 428
2. Fabrics of organic fine substance 428
3. Fabrics in humus mineral soil horizons 429
C. Fabric classifications 434
V. The micromorphology of the most important natural humus formations 435
A. Nonpeaty, submerged humus formations 436

B. Peats 437
1. Primary peats 438
2. Secondary humus formations from peats 439
C. Anmoor 441
D. Terrestrial humus formations 444
1. Raw humus and moder (silicate moder) 444
a) Common properties 444
b) Raw humus 446
c) Moder (silicate moder) 447
2. Rendzina moder 449
3. Alpine pitch moder 449
4. Mull-like moder 450
5. Mull 452
6. Tangel 453
VI. Methods 453
A. Preparatory work 454
1. Sampling in the field 454
2. Methods for the isolation and enrichment of certain components 454
3. Production of microscopic preparations 455
a) Ground thin sections 455
b) Thin sections by slicing techniques 456
c) Debris preparations 456
B. Microscopic investigations 456
1. Techniques of qualitative microscopic investigation 457
2. Techniques of quantitative microscopic investigation 457
3. Microscopic detection methods 458
a) Optical methods 458
b) Chemical methods 459
References 460

I. Introduction*

A. Fundamentals of Humus Micromorphology

Natural humus formations look very different morphologically to the naked eye. These differences provide the basis for a division into groups, which are called humus forms. The morphology of humus forms is determined by environmental factors.

A great variety of morphological forms exist also on the microscopic level. Even humus

* The ground thin sections were produced more or less according to the method of ALTEMÜLLER [1956b] (Vestapol embedding) in the Bundesforschungsanstalt für Forst- und Holzwirtschaft, Reinbek bei Hamburg, Germany (Department of Soil Science, of which W. Kubiena was then the Director). The sliced thin sections, unless otherwise indicated, are paraffin sections covered with Caedax. All photographs were produced by the author. The term "natural size" indicates natural height of the illustration. For horizon symbols compare Section II C (BABEL [1971a]).

formations which appear homogeneous to the naked eye are composed of numerous microscopic constituents that clearly differ in size, color, and form (including internal structure). The constituents may be arranged in a great number of characteristic fabrics. These facts, first observed by MÜLLER [1887], make it possible for microscopic methods to be used in investigations of humus.

The morphological characteristics of the microscopic humus constituents are determined by the physical, chemical, and biotic factors of the microenvironment in which they have developed. The processes brought about by these factors take place on the surface and in the interior of the microscopic constituents. The morphological characteristics of the constituents are thereby altered. Thus the constituents reveal the processes of humus formation.

For example, small aggregates with regular egg-shaped contours indicate the presence and activity of soil animals; they are droppings (German "Losungen"). (This term, borrowed from hunting language, is used in micromorphology for well-preserved excrements of soil animals.)

From the form, size, and spatial arrangement of the droppings one can often draw conclusions about the animal group, and the composition of the droppings may reveal the material that the animals have consumed. By comparing the material of the droppings with the material not yet consumed by the animals, changes caused by the animals can be ascertained.

The organic constituents influence the physical, chemical, and biological interactions in soil. That is to say, they are not only effects but also causes of processes of soil dynamics. Thus, the presence of fungal mycelium suggests the action of fungal ectoenzymes (*e.g.*, Figure 28). A loose arrangement of the solid constituents, which results in a well-developed porous system, facilitates air access and promotes oxidation in terrestrial humus formations.

From the morphology of the constituents, general conclusions about their extramorphological properties can be drawn. Thus, differences in color point to chemical differences. In cork tissue residues, cells with brownish-red contents, as well as those with black contents, often occur. This is the result of chemical—especially oxidative—changes in the cork (Figure 16).

Therefore, in humus research, as in other fields of science, morphology does not only serve the description of an instantaneous state. In the sense used by GOETHE [1807], who in his scientific writings was one of the first to employ the term "morphology," its primary objective is the research on the development of the natural bodies and the principles effective therein. According to KUBIENA [1972], the final object of soil micromorphology is micromorphogenesis.

Since the organic neoformations of the soil develop largely from residues of plants, humus morphological investigations are bound to make use of *botanical morphology*. Analogous to microscopic step by step investigations of mineral weathering (*e.g.*, MEYER and KALK [1964]), the decomposition of the plant residues can be followed step by step from the plant tissues.

This procedure leads to the classification of the organic microconstituents of soils. A botanical identification of the tissue and cell parts can be made, from which the constituents are derived and the description of the type and extent of their morphological transformation is made. But correlations with the categories of humus chemistry, which are deduced from extraction and fractionation experiments, cannot be rigidly made. The results of these two branches of humus research often cannot be compared with each other without special, additional study, because of the diverse methods used in each. Such lignin is detected under the microscope usually by the phloroglucinol reaction. However, in humus chemistry it is generally separated as an acid-insoluble residue.

Because the transformations of plant tissue occupy such an important position in microscopic investigations, restricting the term "humus" to a limited sense would be inconvenient in

humus micromorphology. The term here will include not only the more or less stable substances newly produced in the soil, but all the dead organic matter of the soil (SCHEFFER and ULRICH [1960]). Examples of "humus" are a leaf that has fallen to the ground or a newly cast-off piece of root bark. The microscope shows still another reason why the term "humus" must be used in a broad sense. In certain cases new formations in the soil are scarcely distinguishable morphologically from formations in or on the living plant; they can also be chemically very similar.

Thus, phlobaphenes, which are produced in the living plant, are similar morphologically and chemically to the leaf-browning substances, a great part of which are formed only on the ground and which are very stable humus substances.

It is important in the investigation of the breakdown of plant residues that the development of intermediate substances and end products is linked *topochemically* with the starting structures. This pertains particularly to formations of holorganic humus layers. There the bulk of the organic substances retains most of the basic morphological features (size, form, color, arrangement). With mull, on the other hand, solution processes predominate, and dissolved organic compounds from the plant structures migrate to the mineral fabric components. These organic substances are only recognizable from their color (as components of a color combination). They form pigments of the mineral substance.

B. Applicability of Humus Micromorphology

Micromorphological investigations of humus require solid starting substances and solid topochemically formed end products for the most effective results. Displacements in the solid form, perhaps by soil animals, may also be investigated satisfactorily. The possibilities of humus micromorphological studies are limited when displacement processes in solution or in gaseous form play a role. Little possibility is left for investigation of processes in the molecular region, when these are not manifested in the microscopic region. However, even in such cases indirect relationships may exist.

Thus, the condition and processes of ion sorption on the organic substances are not visible microscopically. There are, however, general empirical relationships between the micromorphologically characterized humus form and its sorption behavior. Correlations between sorption and microscopic features of decomposing plant residues are given by PAULI [1961] and PAULI and GROBLER [1961].

Consequently, humus micromorphological investigations can be applied mainly to organic layers. With mull, on the contrary, the possibilities of their application are more limited, as holorganic constitutents are of less importance in mull. However, fabric investigations of mull may lead to important results, particularly in the field of soil biology.

Humus micromorphological studies can be *preliminary* to other investigations. They can contribute to the knowledge of a material to be treated in some other way and provide clues as to the suitable preparation of this material. The following is an example: In studies on carbohydrates in the organic matter of soil, thin sections of fractions of different grain sizes showed that a considerable part of the extracted pentosans must have originated from fine roots. On the basis of these observations, washed fractions were then prepared and examined separately (ROULET *et al.* [1963]).

Micromorphological investigations are useful in *designing* further investigations in humus biology and humus chemistry.

For the micromorphologically described aggregate formation in mull, soil zoological field studies provided important information. The large rounded, loose-lying aggregates are by no means always derived from excrements (*inter alia*, of earthworms); to a large extent they

are produced by the movements of a great variety of small animals, among them some which do not consume their food in the soil (ZACHARIAE [1962]).

Micromorphological work can be employed to *check* other investigations or be performed to *support* them. VON BUCH [1962] has examined the mechanism of extraction methods by using ground thin sections of fresh and extracted material. KULLMANN [1958] studied the changes of decaying plant roots micromorphologically along with analysis of substance groups.

Micromorphological investigations can be used *independent* of others for studies on *humus formation*. Chemical problems of the transformation of plant substances, for example, can be studied by microscopic methods, especially when histochemical and histophysical techniques are added (*e.g.*, BABEL [1965a]). Model and decay experiments often need not be employed for this, as the multiplicity of factors, which are active in natural humus formations, can be extensively analyzed with the help of the microscope and their effects determined. Therefore micromorphology can test results of chemical or microbiological studies, obtained from model experiments or extracts, with respect to their actual significance in natural humus formation and determine their localization.

Paleopedology and archeology are other fields in which humus morphological studies have been employed. SMOLIKOVA and LOZEK [1969] detected traces of earthworm activity in middle Pleistocene paleosols. ZACHARIAE [1967], by zooecological interpretation of micromorphological findings contributed to archeological discoveries.

Further possibilities of applying humus microscopy are in the field of *forest and agricultural ecology*. It was in studies for classification of humus forms as indicators of site conditions that microscopic methods have been applied for the first time in humus research (MÜLLER [1887]).

BARRATT [1967, 1968a, 1968b] gives micromorphological descriptions of humus forms in relation to agricultural management of grasslands as well as in relation to fertilizing. BABEL and STRAUB [1969] found correlations between stereomicroscopic features and forest management. BENECKE and BABEL [1969], by micromorphological investigations, found differences in the activity of soil organisms in relation to vegetation (spruce forest and deciduous forest). They were interpreted as the result of differences in water and nutrient cycle. Also decomposition processes in composts have been studied by micromorphological methods (ALTEMÜLLER and TIETJEN [1967]).

In close relation to this field is the application of humus microscopy in studies on the *ecology of soil organisms*. It is microscopic investigations of humus profiles that reveal the habitat of the decomposer organisms and the scene of the decomposing processes in ecosystems. Soil zoologists apply thin section techniques for studies on the positions and feeding behavior of soil animals (*e.g.*, ANDERSON and HEALEY [1970]). Soil microbiologists perform direct microscopic observations of soil particles for studies on localization of bacteria and fungi in their natural habitats (*e.g.*, GADGIL *et al.* [1967]).

The following account emphasizes the results of direct investigations of soil organic matter by light microscopy. In some cases results of electron microscopy are included. Other investigations, such as chemical, zoological, and microbiological, are only cited for discussion of morphological findings.

II. Survey of the Microscopic Structure of Humus Formations

Generally, ground thin sections give the best picture of the microscopic structure of a humus formation. In a typical case the following groups of constituents are found. At low or medium magnification fairly large particles are seen, which are often strikingly colored and

easily recognizable as plant residues. Between them lies a material that is distinguished from the plant residues by its much more finely divided, irregular, and often denser structure; it usually has darker colors. This material is often formed from regular egg-shaped or cylindrical aggregates, sometimes with racemose knobbly contours. These are the droppings of soil animals. At a somewhat greater magnification thin brown fungal hyphae can be seen. In addition, mineral grains are found; they are usually pale or colorless. Often they are accompanied by a yellow-to-brown fine substance. Crossed polarizers show that it consists of mineral particles bound together by colored isotropic materials. Within and between these different groups of solid substances, air-filled pores of the most varied shapes and sizes are developed, (*e.g.*, Figures 1, 2). These parts are not distributed at random but exhibit a more or less obvious pattern.

Investigations with numerous illustrations of microscopic humus preparations are: BAL [1973] (69 microphotographs, 16 in color); BABEL [1972b] (21 microphotographs of moder horizons); BARRATT [1968/69] (12 semidiagrammatic drawings); GEYGER [1967] (19 small microphotographs); FRERCKS and PUFFE [1964] (36 small microphotographs of secondarily decomposed peats); GROSSE-BRAUCKMANN and PUFFE [1964] (21 small microphotographs of peats); HARTMANN [1952] (about 45 microphotographs); HARTMANN [1965] (79 micro- and semimicrophotographs, 56 of which are colored); KUBIENA [1944] (32 illustrations); KUBIENA [1948] (about 25, some of them colored illustrations); KUBIENA [1953] (16 semidiagrammatic drawings); KUBIENA [1970] (about 25 colored microphotographs; PUFFE [1965] (36 small microphotographs of peats); PUFFE and GROSSE-BRAUCKMANN [1963] (50 small microphotographs of peats); VAN DER DRIFT [1964] (16 small microphotographs); and ZACHARIAE [1965] (18 large microphotographs).

A. The Constituents

Constituents are defined here as individual constituents (structural units of the lowest level). The three groups already mentioned are described under the terms "plant residues," "organic fine substance," or, where no confusion can arise, simply as "fine substance" and "mineral constituents."

1. *Plant Residues*

The term "plant residue" means coherent tissue parts, which are recognizable, as such, microscopically. They show distinct cell structures or distinct contours of plant organs or both. The plant residues could be designated purely morphologically as organic skeletons. This is mechanically correct. However, from the viewpoint of soil dynamics, plant residues are not inert, but undergo much more vigorous and more rapid conversions than does, as a rule, a mineral soil skeleton.

The plant residues reveal quite clearly their origins from the different plant organs and tissues. Leaf and needle residues are naturally frequent. Residues from fine roots also often occupy a large share of the microscopic picture. All other plant residues that reach the soil can also be recognized in the first stages of disintegration from histology. Most frequently among these are pieces of wood and bark residues.

The structures of the tissues in plant residues are deformed to varying extents and in various ways. Yellow, brown, or red parts appear. These "rotting products" were often termed "humolignins" in the older literature (MAIWALD [1939]). Their identification and interpretation can be given on an histological basis (see Part III).

2. *Organic Fine Substance*

The term "organic fine substance" is used here to mean organic material without definite

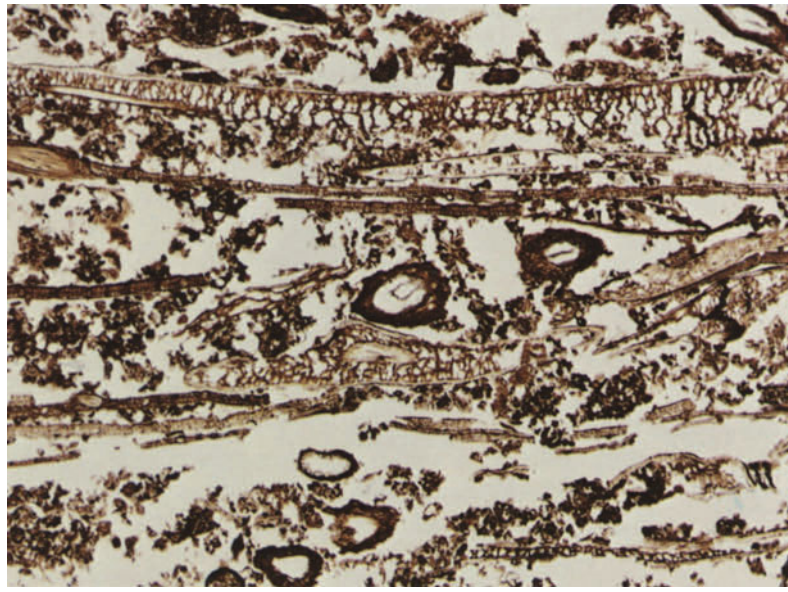

Figure 1. Decay layer (F_m) of a moder. Horizontally lying leaf residues (narrow) and needle residues (broad, thus top, one occurring longitudinally; somewhat below the center, an obliquely occurring needle). Root residues (*e.g.*, in the center, two examples transversely; mainly cortical parts are intact). A part of the fine substance shows indistinct (granular), more rarely, egg-shaped droppings. Colors of the fine substance, from bright reddish brown to black. In the fine substance fungal hyphae (indistinctly recognizable at this magnification). The residues of needles and leaves still form a laminated fabric in places (bridges of fine substance); in places greater areas of fine substance occur, forming loose to dense clusters. Wet moder under *Abies*, *Pinus* silv., *Fagus* forest (Black Forest, Germany). Ground thin section (25 μm), bright field, natural size 4 mm.

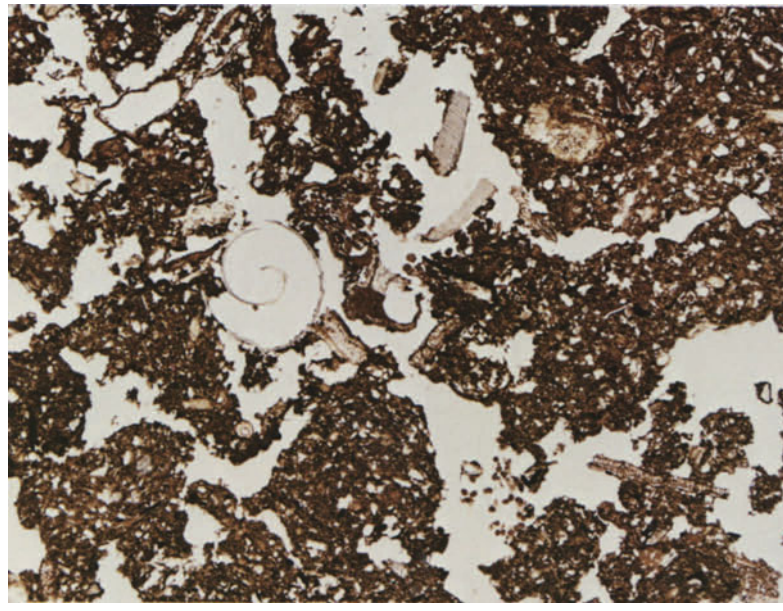

Figure 2. Mull, spongy fabric. Irregularly formed, combined aggregates (more or less altered droppings ("castings") of earthworms) with many plant residues, which are mixed into the mineral soil largely by earthworms (pieces of wood, leaf fragments (below, right-hand side), root residues, etc.). The plant residues have been disintegrated partly by mites (droppings, *e.g.*, in the center.) The mineral substance contains quartz and calcite grains (the quartz grains here appear like holes in the fine substance). The mineral fine substance is colored by organic matter. Rendzina-mull under beech, A_{hh} (4 cm) (Swiss Jura). Ground thin section (25 μm), bright field, natural size 5.5 mm.

microscopically recognizable structures. Cell wall fragments, single cells, fungal hyphae and very small pieces of tissue which comprise only a few cells are also included in the definition.

The organic fine substance is produced from plant residues by disintegration and shows little or none of the original structures, or it may be formed from precipitates of dissolved organic substances. The parts have irregular fine-grained and fine-foliated forms and usually an irregular flocculent arrangement. Their colors are sometimes pale, like those of the initial tissue, less frequently bright (yellowish red, brownish red), and mostly dull, dark, and often black. As to the sizes of the individual particles, the size of the particles of the fine substances is usually in sharp contrast with the plant residues. Nevertheless, a definitive threshold size cannot be given, since the size is dependent on the disintegrating agents. In general, the threshold size lies at about 100 μm.

3. *Mineral Constituents*

As a rule, mineral constituents are of essential importance to natural humus formations. This is true for the mineral skeleton, which influences especially the physical conditions of humus formation and on which chemical effects of humus can also become manifest. Mineral fine substance may react with dissolved organic substances to give a stable complex, the so-called clay-humus complex. In this the humus cannot be recognized in microscopic constituents of its own.

In addition to these solid constituents there are also pores filled with air or water.

B. The Fabric

The term "fabric," which was first introduced by KUBIENA [1935, 1938], is defined by ALTEMÜLLER [1962b] as the arrangement of the constituents with respect to form, function, and genesis.

The natural humus fabrics are built of varying proportions of the constituents which may be arranged in many different ways. Fabric analysis describes the mutual arrangement of the constituents (elementary fabric) as well as the size, shape, and arrangement of aggregates and pores. Plant residues often are interconnected with each other by fine substance or fungal hyphae. The fine substance is often aggregated in droppings. Droppings can be interconnected with each other. Coherent masses of fine substance without aggregation are found also. Mineral constituents can be arranged without connection with the organic fine substance (moder, Part V D 1); in other cases mineral and organic constituents are loosely aggregated with each other (mull-like moder, Part V D 4); finally clay can be pigmented by organic substance, without intrinsic organic particles being visible microscopically (mull, Part V D 5).

Natural humus horizons show a number of fabric types, which are found repeatedly. Horizons built up by plant residues prevailingly often show a laminated fabric. Horizons of organic fine substance sometimes reveal a dropping fabric. This is found in humus mineral soil horizons also. Under different conditions there, a spongy fabric is formed.

Fabrics of humus soil horizons are formed by action of biological and nonbiological forces. By fabric analysis, therefore, physical and biological soil conditions can be investigated.

C. The Profile

Most humus formations have a profile differentiated into horizons that can be detected macroscopically. This is particularly distinct with terrestrial superficial humus forms (raw humus and different forms of moder). The horizons of such a humus profile illustrate the successive transformation stages of the litter. Increasing depth in the profile corresponds to

increasing age of the organic components. Since the breakdown of the plant residues can be detected microscopically, no model decay experiments need be constructed.

Naturally there are always minor discrepancies in this correlation between age and depth in the profile. They are usually caused by irregularities in the subsoil or by rather gross mechanical effects which are brought about, among other things, by large animals. Besides, there are some spatial fluctuating differences which are attributable to the uneven distribution of soil animals and microorganisms. With humus forms other than the terrestrial superficial humus forms, for example, mull and fen-mull, the correlation between age and depth is not so clear, because the processes are intrinsically more rapid and because of the mixing action of the soil animals.

Fabric analysis shows variations in proportions of constituents within the profile. In a beech raw humus, for example, the amount of recognizable leaf residues decreases and the amount of fine substance and fine roots increase with increasing depth. In the deeper parts, mineral grains begin to appear (BABEL [1965a]). Correspondingly, the fabric type changes altogether. The laminated fabric of the upper parts becomes transformed into a fine substance fabric and finally into an agglomeratic fabric.

The constituent analysis reveals other changes with increasing depth. In the plant residues, progressively larger amounts of brown substances are generally formed, the tissue structures are gradually lost, and some tissue parts disappear altogether. The fine substance also changes its color with depth (see Part III).

Macromorphologically these differences lead to the differentiation of the humus profile into three layers, as first described by HESSELMAN [1926]:

L layer (or L horizon, litter layer, förna): The more or less loose deposit of the plant cover litter, which, after its accumulation on the soil, is not yet or is only slightly changed morphologically.

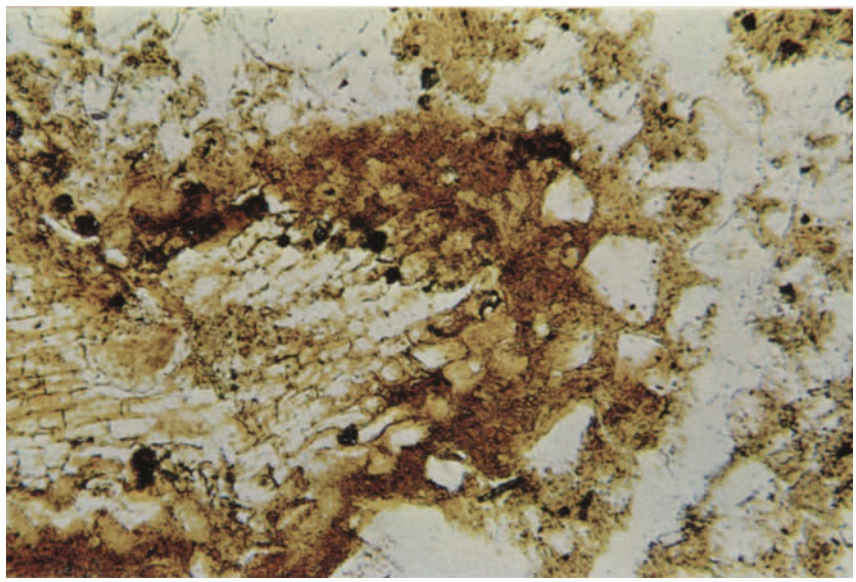

Figure 3. Iron oxide encrusted root residue in pseudo-gley, A_h. The iron oxide penetrates into the tissue. (The root is sectioned through the cortical tissue, oblique.) Colorless regions in the iron crusts are quartz grains. Ground thin section (30 μm), bright field, natural size 500 μ.

F layer (fermentation layer, decay layer): The layer in which more or less disintegrated plant residues as well as increasing amounts of organic fine substance occur.

H layer (humus substance layer): The layer consisting almost entirely of fine substance. Except root residues, plant residues are not recognizable macroscopically and microscopically or only in small amounts.

Below there is a mineral humus horizon (A_h) in which organic as well as mineral constituents, or even organic substance as a pigment of the mineral, are present.

According to a new proposal of BABEL [1971a, 1972b], these horizons can be subdivided further: L_n (n: new), L_v (v: German "verändert" analogous C_v), F_r (r: plant residue), F_m (m: medium ratio plant residue: fine substance), H_r (r: plant residue), H_f (f: fine substance), A_{hh} (hh: rich in humus), A_{hu} (part of A_h under A_{hh}). These horizons were defined by their plant residue/fine substance ratio (except for L_n with L_v and the A_h horizons) (see Part V D 1a).

The horizons of the humus profile, which are defined purely morphologically, have characteristic dynamics (*e.g.*, LEHMANN, MEYER, and SCHONLAU [1969]), detailed work on which is one of the chief objectives of humus micromorphology (*e.g.* BABEL [1972b]).

The sequence of L, F, H, and A_h horizon is not developed in all humus profiles. Any of these four horizons may be missing.

In a special case, namely with secondary humus formations from peats, a fermentation layer can follow below the humus substance layer (see Part VB2).

III. The Organic Constituents of Humus Soil Horizons

A. Animal Residues

While the activity of animals in the breakdown of plant residues has been extensively studied, little is known about the occurrence of residues of soil animals as constituents of natural humus formations or about the phenomena of their decomposition. Therefore, only few data can be presented here. On the whole, animal residues are seldom found in microscopic preparations of humus formations.

MÜLLER [1887] found pieces of chitin from soil animals in debris preparations of the humus substance layer of moder. Shells of thekamoebae can often be observed in ground thin sections of moder and raw humus formations. Mollusk shells may be found fairly often, especially in submerged and semiterrestrial humus formations (see Figure 2). According to KÜHNELT [1961], brown substances can be observed occasionally in their interior as decomposition products of the soft parts. Chitin residues of insects in the soil are often attacked by actinomycetes and by molds, according to KUBIENA [1938, p. 226 ff]. See also microbiological studies on this subject by OKAFOR [1966], where bacteria and protozoa have been found growing on insect wings in the soil. Chitin residues, being influenced by microorganisms, become colored dark brown to black in this process. The decomposition products of animal plankton also give very dark colorations. The details of the colonization of animal residues by microorganisms and the type of their decomposition, as in the case of plant residues, are dependent on the humus form (KUBIENA [1938]). In the hydrobiological literature, there are studies on the breakdown of animal chitin in submerged soils (RUTTNER [1962]). In thin sections sporadic particles occur that may probably be assumed to be animal residues, especially chitin fragments. They are usually colored yellow, with regular outlines, and often show primary fluorescence. (Colorless particles sometimes become recognizable only by their fluorescence, BABEL [1972a].) Many animal residues show (with reference to the longitudinal axis) partly positive and partly negative birefringence. Round particles, which might be the cases of eggs or cysts, may also be found. Cysts were identified by SEKERA [1956] in debris

preparations. In such preparations, which are better suited to investigations of this kind than ground thin sections, other animal residues (*e.g.*, tarsal joints of arthropods) may also be recognized.

Animals that were still living when the sample was taken are found very seldom in normal ground thin sections of soils. BABEL [1972a], by fluorescence microscopy, found the body of an enchytraeid. Soil zoologists have developed agar or gelatine-embedding techniques for studying animals in their natural positions (*e.g.*, ANDERSON and HEALEY [1970]).

The number of animals and animal residues that may be found in ground thin sections of humus formations is much smaller than would be expected, considering the short life span of most animals and the large animal biomass, which is about 15 to 500 g/m^2, according to KÜHNELT [1961].

This cannot be explained simply by the fact that many of the large soil animals escape during sampling and the smallest forms can scarcely be recognized in thin sections. Arthropods, most of which should be found in thin sections, are present in amounts of the order of 10 g/m^2 (MACFADYEN [1963]); but they are also found more seldom in thin sections than would be expected from calculations.

This circumstance indicates the ease of decomposition of animal residues. Many animals shrink beyond recognition during drying which precedes the embedding of the sample in synthetic resin (MINDERMAN [1956]). In the soil, animal corpses are consumed often very soon by carrion feeders (KÜHNELT [1961]). The decomposition of animal chitin by the microflora of a humus substance layer has been demonstrated in laboratory experiments (GRAY and BELL [1963]). It may be assumed that breakdown products of animals and new formations from those in the organic fine substance or in the organic pigment of mineral soil are quantitatively significant as stable humus substances. However, this cannot be proved micromorphologically, at least in investigations of natural humus formations. In model experiments on the decay of combined plant and animal residues, SEKERA [1956] was able to show the importance of animal residues in the formation of stable humus substances.

B. Plant Organ and Tissue Residues

Plant organ and tissue residues are here briefly termed "plant residues" (see Part II). Their descriptions are related to the *histology* and *organography* of the fresh parent material. Information is thereby obtained, as discussed in the introductory sections, not only on the morphological changes, but also on the material transformations that occur in the course of humus formation (see Section I A).

The general structure of the fresh tissues and organs is quite well known from botanical studies. The unique structure of the original materials in a given instance, however, often needs to be determined, because botanists' investigations are usually limited to either teaching examples or technologically important material.

METCALFE and CHALK [1950] and METCALFE [1960], who deal with the anatomy of the taxonomic groups of plants in concise accounts, are exceptions; KIRCHNER, LÖW, and SCHRÖTER [1908] also frequently provide detailed anatomical data. Another useful textbook is LINSBAUER [1922]. Introductions to the anatomy of plants are given by ESAU [1953] and HUBER [1961]. The plant cell wall is dealt with by FREY-WYSSLING [1959] and ROELOFSEN (in LINSBAUER [1959], who refer to its morphology, biochemistry, and biophysics. The microscopy of wood and bark may be found in FREUND [1951, Vol. 5]. SCHRÖDER [1952] describes the roots of about 100 bog and grassland plants. The morphology of fungi, the plectenchyma of which are often seen in soil thin sections, is presented by LOHWAG [1941] and BARNETT [1953].

The *taxonomic determination* of the plant species, from which an organ residue or tissue

residue originates, is, in general, only of interest secondarily or indirectly—as, for instance, for comparisons with the parent material. If one investigates the vegetation of the site concerned and its undecomposed or slightly decomposed litter, it is usually very easy to determine the plant species related to the residues.

More difficult cases are the older humus formations, which have been produced from other than recent vegetation. This happens frequently in the deeper layers of peat. There the taxonomic determination of the plant residues is done by so-called *coarse residue analysis*. Here, as in pollen analysis, the scientist attempts to reconstruct the former vegetation. If the typical characteristics of the residues are not recognizable macroscopically or under the magnification of a hand lens, then coarse residue analysis has to depend, among other things, on the microscopic structure of the wood, the shape of the epidermal cells or of the cuticula ("cuticular analysis"), the stomata, hairs, or on other characteristic microscopic features (see the botanical literature quoted above). Decomposition phenomena are never considered more than superficially in such investigations, which are orientated toward vegetation history.

For identification after mechanical isolation and purification, the coarse residues are clarified chemically with sodium hypochlorite, potassium hydroxide, or oxalic acid (HOFMANN [1934], WILLERDING [1960]). Methods for the light microscopic determination of fossil charcoals are found in MÜLLER-STOLL [1936]. FIRBAS and BROIHAN [1937] have determined the spruce fraction in the formation of the different horizons of a raw humus cover by enumeration of the stomata from spruce needles. GROSSE-BRAUCKMANN [1964] has described and determined coarse residues from peats. Literature on coarse residue analysis with reference to vegetation history is given by FIRBAS [1949].

In humus research the successive stages of decomposition of the plant residues are of interest. The plant residues concerned can be isolated under the stereomicroscope from the successive horizons of the humus profile. For further investigation they are sectioned by microtome (BABEL [1964a]).

1. *The Parent Material*

In forests, *leaves* and *needles* are the most important parent material for humus formation. As a rule they amount to more than 80% of the litter. The remainder comprises pieces of *twigs*, *bud scales*, *fruits*, and *stems* from ground vegetation. (A detailed analysis of the litter of an oak forest is given by BURGES [1967]). Brushwood and timber lying on the soil in undisturbed natural forests equal the amount of litter. In forests under management, little brushwood and timber accumulate. Beside the litter, roots constitute an important part of the parent material. Root production in forests normally may be about a fifth of the total litter production (SCHLENKER [1962]) for southwestern Germany. But this amount varies greatly with environmental conditions. Sometimes roots predominate as parent material (Figure 12); WILDE [1958] then speaks of "rhizogenic humus."

In the upper H horizon of a beech raw humus in northwestern Germany, dead roots constituted 6.3% and living roots 9.6% of the total mass (VON BUCH, personal communication; see also VON BUCH [1962]). In this profile the maximum density of living root tips (which was in the F horizon) was 90 times as high as the maximum density in a mull profile (MEYER [1967]).

In grassland, DAHLMAN [1968] found the root production to be about as high as the shoot production. The same author determined the average life duration of roots in a grassland ecosystem to be about four years; similar results are found by ORLOW [1968] for the life duration of roots in a pine forest.

The organs mentioned consist essentially of three groups of tissues, namely, parenchyma, phlobaphene-containing tissues, and lignified tissues. The decomposition of the tissues shows

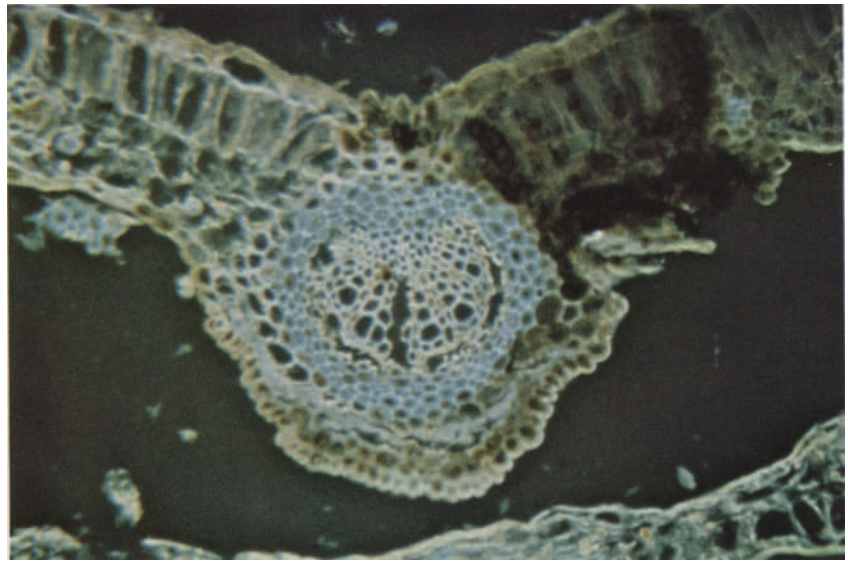

Figure 4. Beech leaf vein (cross section), isolated from L_n horizon, fluorescence illumination. Blue ring: sclerenchyma (primary fluorescence of lignin). In the xylem are distinguishable undecomposed, whitish blue fluorescing cell wall parts from decomposed, yellow appearing ones. Strong fluorescence of the lower cuticula. Top left, fluorescence of parenchyma cell walls readily visible; top right, it is masked by browning substances and fungal pigments. Raw humus (Northwest Germany). Sliced section (glycerine, 10 μm), unstained, fluorescence illumination, natural size 300 μm.

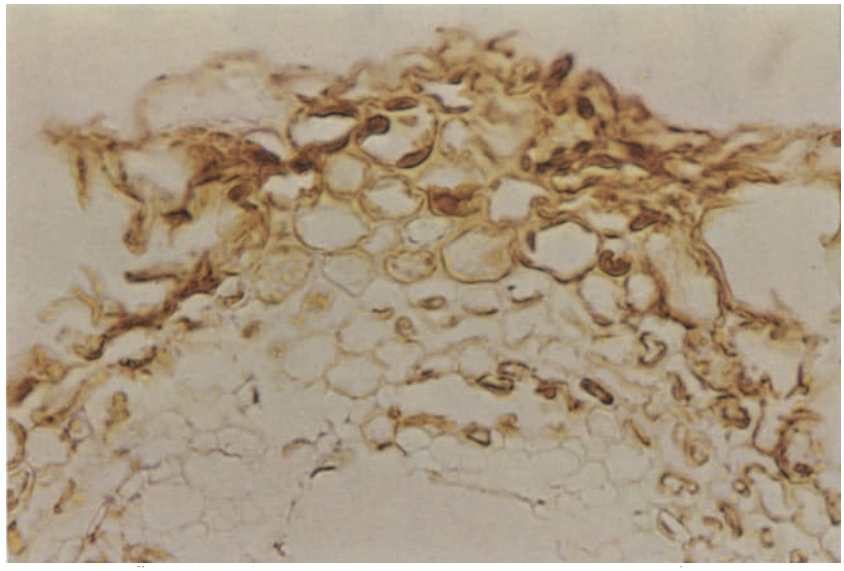

Figure 5. Beech leaf (cross section), isolated from F_m horizon of a raw humus. Upper half of the leaf vein. In the middle of the picture from the top downward, the following tissues: Epidermis (one cell layer, badly focused), collenchyma (about four layers, remaining cell walls yellow; brown bodies and yellow granular substances are remains of the secondary wall), sclerenchyma (about three cell layers, the colorless middle layers of the cell walls are more or less intact, the yellow substances on them as well as the brown rings are remains of the secondary wall), phloem (the small hole with yellowish brown substances on the edges, somewhat under the center of the picture), xylem (1 or 2 layers, remaining only the colorless middle layers), on the under edge of the picture the disappearance of the medulla-like central part of the xylem has left a great hole. (Northwest Germany) .Sliced section (10 μm), bright field, natural size 100 μm.

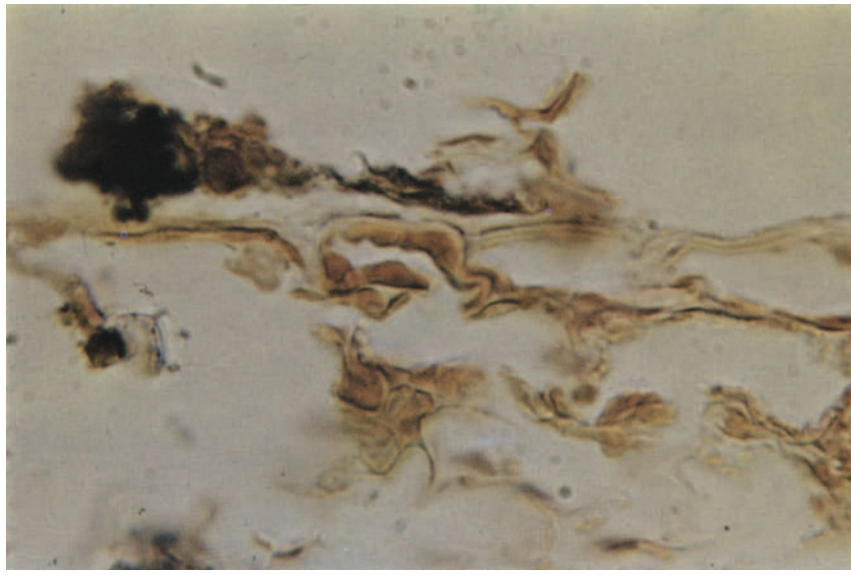

Figure 6. Dark bodies of probably microbial origin on the residues of the epidermis of a beech leaf. Epidermis outer wall colorless, epidermal cells from the inside encrusted with yellowish brown leaf-browning substances. Isolated from raw humus, F_m (Northwest Germany). Sliced section (10 μm), bright field, natural size 45 μm.

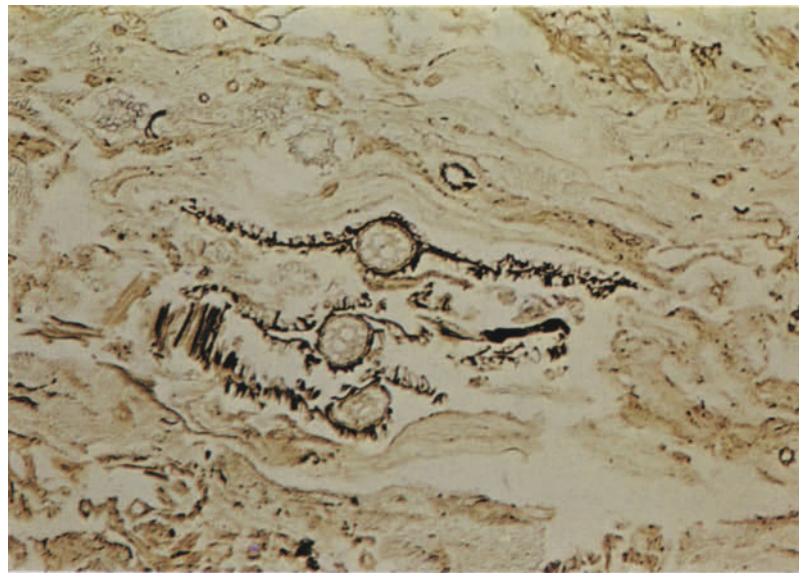

Figure 7. Sphagnum peat with residues of higher plants. Three-leaf residues of *Eriophorum vaginatum* with vascular bundles which are hardly altered, the parenchyma has changed to dark brown substances. Between the almost colorless sphagnum residues are yellow substances, part of them formed out of the solution state (compare Figure 29). Sliced section (Cremolan method, 10 μm), bright field, natural size 1.1 mm. (From a preparation by D. Puffe, Bremen.)

common features within each of these groups (BABEL [1965b]). (Brief details on the chemistry of the plant substances cited in the following are to be found in Section III B 2 bγ, cγ and dδ).

Parenchyma forms the green tissues of leaves, the cortex of young twigs and fine roots, and the cortex and medullary parts of the stem. They are built up from living cells; these have thin cellulose walls, a protoplast consisting mainly of protein, and a vacuole.

Phlobaphene-containing tissues give external protection to many organs. They include older or outer portions of the cortex, and most of the varied tissues of the bark of roots, twigs, and stems, especially cork tissues (periderms). The cork tissues are easily recognized by the regular parallel row arrangement of the rectangular cells. The tissues of many bud scales and fruit cases and seed cases also contain phlobaphenes. These tissues sometimes have thin cellulose walls, but usually they have thickened walls that, in the cork, are formed as a rule from middle lamella, suberin lamella, and carbohydrate lamella. Middle lamella and carbohydrate lamella can store lignin, but never suberin (MADER [1958b]). The phlobaphene-containing tissues contain dead cells while the plant is still living. The cell lumina contain yellow brown, or red tannin oxidation and polymerization products which have been formed following the death of the cell. These are termed *phlobaphenes.* In the so-called tannin cork the whole lumen of the cells is filled with phlobaphenes. In other outer tissues smaller amounts of phlobaphenes occur. The cell walls, especially the suberinized ones, are likewise occasionally colored by phlobaphenes (Figure 15).

Lignified tissues not only form the main mass of the woody parts of the wood growths but occur also as consolidating elements (sclerenchyma) in stalks, leaf epidermis, leaf hypodermis, leaf veins, and bark. The xylem of the vascular bundles is also lignified. The lignified cells are dead even in the living plant. Their lumina are nearly always empty. The cell walls are about 1 to 4 μ thick—much thicker therefore than those of the parenchyma. Under the light microscope at least two wall layers, the middle layer and the secondary wall, can be distinguished (Figure 4).

The middle layer may be differentiated electron microscopically into the middle lamella and the primary wall. The secondary wall, which forms by far the thickest wall layer, often shows a laminated structure. On it another thin wall, the tertiary wall, is deposited. The middle lamella consists of pectin. The primary wall consists of cellulose fibrils in a loose scattered texture, and the secondary wall consists of cellulose fibrils in a dense parallel texture. In all these layers lignin is deposited as an incrustation, and distinctly more so in the middle lamella and primary wall than in the secondary wall (RUCH and HENGARTNER [1960]). The lignin content is highest in the intercellular spaces. The tertiary wall apparently consists mainly of pectin, carbohydrate fibrils, and denatured residues of the cell contents (FREY-WYSSLING [1959]). There are chemical differences between the lignin of different plants and different kinds of tissues. They may be detected, for example, by the different methoxyl contents, and they often show different behaviors on degradation (SCHEFFER and ULRICH [1960], THOMPSON *et al.* [1964]).

In addition to these three groups, there are some other tissues of lesser importance quantitatively as parent materials for humus formation. The *epidermis* in leaves and stalks warrants consideration. It is similar to the parenchyma; however, the cells have a thickened outer wall which, starting from the cell lumen, consists in general of a rather thick cellulose layer, a pectin layer, and a cuticular layer. Across these three layers the cuticula can be separated as an outermost thin layer. The two last-named layers, which may also together be termed cuticula in the broader sense, are usually only $\frac{1}{2}$ to 1 μ thick combined. At the needles of coniferous trees, however, their thickness amounts to several microns. The cuticular layer consists of cutin, pectin, and cellulose; the cuticula proper consists of cutin only. Furthermore,

waxes can occur in the cuticular layer, and also on the surface of the cuticula (FREY-WYSSLING [1959]).

Collenchyma are thick-walled tissues of living cells. They occur in leaf stems and leaf veins as well as in the stalks of herbaceous plants. The cell walls are distinguished by a high pectin content and by the poor order of the cellulose fibrils, as may be gathered from their shrinkage in dehydrating agents and from their weak birefringence. Under certain conditions it can be established that the secondary walls of the collenchyma consist of alternating lamellae of pectin and cellulose (FREY-WYSSLING [1959]).

The *phloem* of the vascular bundle and of bast contains, in addition to parenchymatous elements, the sieve tubes, which are thin-walled cells rich in hemicellulose (callose). Finally, *pseudotissues* (plectenchyma of fungi) should be included here. They are frequently found in soil thin sections—especially of dystrophic humus forms (see Part V)—in the form of dark-colored sclerotia and mycorrhiza mantles, and more rarely in the form of fruiting bodies. The framework substance of cell walls is chitin. The brown pigments are often collectively called melanins. They can constitute up to 54% of the mycelial weight (SCHEFFER and ULRICH [1960]) (Figures 20, 21).

Typical *chemical analyses* of humus parent materials might give, for straw, 5% crude protein, 40% cellulose, and 20 to 25% lignin. Forest litter might have about 5 to 15% crude protein, 15% cellulose, and 20% hemicellulose (SCHEFFER and ULRICH [1960]). The lignin content of the autumn foliage of different forest trees, according to STÖCKLI [1952], amounts to between 13% (*Castenea*, or chestnuts) and 27% (*Abies*, or firs), when determined with thioglycollic acid.

2. *The Decomposition of Tissues*

(a) General Phenomena

Changes in the decomposing tissues to the point of loss of coherence of the tissues will be discussed in this section. Even while the coherence of the tissue is maintained, manifold decomposition phenomena are shown in their interior as discolorations and deformations of the cell components. Later on in the train of breakdown processes, cracks, holes, and other flaws are formed, and finally the coherence of the tissues is completely lost. These symptoms arise in part through nonbiological processes, such as swelling, shrinkage, and the collapse of thin-walled tissues (for example, of the phloem). For the most part, however, they are formed by the activity of plant microorganisms and especially of animals (for further details, see Part III C 1).

The different tissue groups are destroyed at varying rates by these agents. The following order of increasing resistance, although somewhat schematic, is frequently valid: phloem, collenchyma, parenchyma, lignified tissue, epidermis, phlobaphene-containing tissue (Figure 12). This series is brought about essentially by different chemical and biotic activities in the tissues (different nutrient contents, special resistance to degradation of certain plant substances) and by mechanical differences (hardness and small water uptake by tissues of thick-walled cells). The difference in rapidity of destruction of parenchyma and lignified tissue is often striking, even macroscopically.

This is seen, for example, in the skeletonization of the leaves of deciduous trees. The lignified tissues of the leaf veins remain behind as the leaf skeleton after decomposition of the mesophyll (WITTICH [1939], FÜHRER [1961], ZACHARIAE [1965]). Similar phenomena are described by BARRATT [1965] in the decomposition of grasses and herbs. KULLMANN [1958], KONONOVA [1961], and JABLONSKI [1963] have made corresponding observations in decay experiments with fodder plant residues, and GRAFF [1955] in the case of destruction of straw

by arthropods. The same conditions also apply to plant residues from peats; but in this case it should be noted that their decomposition has occurred not in the process of peat formation, but previously, under aerobic conditions (GROSSE-BRAUCKMANN [1963]).

The sequence outlined holds when conditions are favorable for breakdown, that means, in mull. Under other conditions deviations can occur. The observation by HANDLEY [1954] that, in raw humus, the mesophyll of *Calluna* leaves may remain intact longer than the veins is very important to the problem of raw humus formation.

The morphological decomposition phenomena which go on within the still coherent tissues seem, on the contrary, to proceed very similarly in different humus forms. Any variations are chiefly in rate of decomposition. (These ideas mainly have been obtained from investigations of the author on oligotrophic and dystrophic humus forms).

The breakdown products of tissues are solid, liquid (solutions), or gaseous. Only those decomposition products or residues that are solid can be examined microscopically. However, they may often be contaminated by organic substances, or rarely by mineral substances, from the solution phase, which have diffused into them or have been deposited on them as thin crusts. This possibility has to be considered with all humus forms, especially in the strongly decomposed horizons. As a rule, however, the contaminating substances cannot be detected morphologically with certainty. Only occasionally are rather thick organic crusts from the solution phase formed around plant residues, which are easily recognizable as such (Section III C 2 e). Frequently, of course, the dissolved substances are lost from the horizons investigated.

Experiments by NYKVIST [1963] show that the proportion of water-soluble substances in the litter may be assumed to be quite high. From needles, 1% of the dry weight may be leached out; from leaves, 4% (beech) to 17% (ash). Furthermore, there are the well-known brown seepage waters which often occur on the profile walls of podsols. ZIECHMANN and PRZEMECK [1964] have estimated in such a solution a concentration of 0.3 g organic matter per liter of solution. The uniform brownish-black coloration of a fossil wet moder is probably due to such solutions (Figure 14). KÜHNELT [1961] mentions a yellow coloring of wood as a result of infiltration of solutions from the dark droppings of diptera larvae.

The occurrence of *gaseous decomposition products*, arising during mineralization, can be inferred micromorphologically only indirectly, if at all, and in its morphological symptoms—namely, the disappearance of cell or tissue parts—cannot be distinguished from the dispersal of dissolved substances. However, sometimes solidified bubble-shaped, gas-filled pores that have been formed by putrefaction gases can be found in sections of sapropels.

MEYER [1960], from incubation experiments, has calculated that 60 to 80% of the organic matter is mineralized down to the lower limit of the fermentation layer of a mull. HOLLING and OVERBECK [1961] have computed a substance loss (in solution or gaseous form) of 33 to 80% for sphagnum peats, appearing macro- and microscopically only slightly or moderately decomposed.

(b) Parenchymatous tissues

(α) *Morphology.* Parenchymatous tissues often disappear rapidly and without residues (Figure 33). This was observed particularly in decay experiments, in which optimal conditions for decomposition are established—as, for example, by KONONOVA [1943] with the cortex and medulla of lucerne roots. In grass roots, which died off, the cortex sloughed off and disappeared, leaving only the central stele (GADGIL [1965]). GROSSE-BRAUCKMANN and PUFFE [1964] obtained corresponding results with the decomposition of parenchyma in peat. GROSSE-BRAUCKMANN [1963] in a similar study found differences in the rapidity of decomposition of parenchyma of various groups of mosses. Hepaticae decompose most quickly, followed

by musci and finally sphagnum. The central parts of the moss stem decompose more quickly than the outer, cortex-like portions. This might be attributable to chemical differences in the composition of the cell wall. In mosses from peats small amounts of newly formed brown substances were found occasionally (GROSSE-BRAUCKMANN [1963]). KONONOVA [1961], in decay experiments with clover leaves, showed that brown water-soluble substances had been formed in the interior of parenchyma cells by autolysis of myxobacteria, which previously had shown an abundant development in the parenchyma, along with the consumption of the cell content substances. TRIBE [1963], in decay experiments with lettuce leaves, found dark spherical bodies which had apparently been produced from the contents of the mesophyll cells.

In the mesophyll of leaves and needles of forest trees, on the contrary, water-insoluble encrustations of the cell walls are formed (GROSSKOPF [1935], HANDLEY [1954], BABEL [1965a, b, 1972b]). Objects of intensive study were leaves of *Fagus* and *Calluna*, as well as needles of *Picea* and *Abies*. The crusts are brown, partly yellowish and partly reddish (Figures 10, 6). When present in large amounts, these substances can form spherical bodies (Figure 9). They appear immediately after the death of the cells, hence frequently even before leaf fall. During the first months on the soil, they develop further. They are here termed *leaf-browning substances*. The formation of browning substances may also be observed in other parenchyma as well as in plants other than those named. It seems to be the first step in the normal case of parenchyma decomposition.

Leaf-browning substances such as lignin can be stained with gallocyanine (GROSSKOPF [1935]). They are soluble in sodium hypochlorite (eau de javelle). After their removal, the remains of the cell walls are revealed, which, in early stages, scarcely show any decomposition symptoms and in which cellulose can still be detected by birefringence and reaction with chlorozinc iodide. This detection is possible to a limited degree or not at all unless the leaf-browning substances are removed.

Even before the loss of tissue coherence, a color change of the browning substances to dark brown may take place (Figure 8). This phenomenon was associated with a chemically detectable cellulose degradation in experiments by FALCK [1930]. It would be analogous, therefore, to the brown rot of wood. On the contrary, HANDLEY [1954] was able to show that cellulose is protected mechanically and possibly chemically from degradation in the soil by "masking" with browning substances. In raw humus, residues of cellulose walls encrusted with leaf-browning substances persist in the humus substance layer (HANDLEY [1954], BABEL [1965a]).

A part of the leaf-browning substances, however, disappears in the lower part of the L horizon (L_v, see Section II C). This is shown macroscopically in a striking clarification of the leaves. (Compare BABEL [1972b] for illustrations). The fully preserved leaves change to a clear yellow color, sometimes on the entire blade, and sometimes only in restricted areas. Microscopically somewhat the same picture is found as after treatment with sodium hypochlorite. All the colored substances in the mesophyll disappear and the slightly altered cell wall residues become clearly visible (Figure 8).

In other cases, however, the cell walls seem to disappear simultaneously with the decomposition of the leaf-browning substances, so that the entire leaf or the whole needle collapses, leaving only the epidermis, hypodermis, and vascular bundles. (Figure 33). Macroscopically such leaves appear to have become thinner and the needles appear shrunken (MEYER [1962], BABEL [1972b]. In the breakdown of the cell walls of the parenchyma, net-like and perforated decomposition phenomena have been observed in a few cases (ALTEMÜLLER and BANSE [1964] with straw, GROSSKOPF [1935] with pine needles). Whether the cell walls themselves are colored is difficult to establish clearly in the presence of the encrusting browning substances; after sodium hypochlorite treatment, they are colorless. The light refraction and birefringence of the morphologically fully intact cell wall regions apparently remain unchanged. In addition,

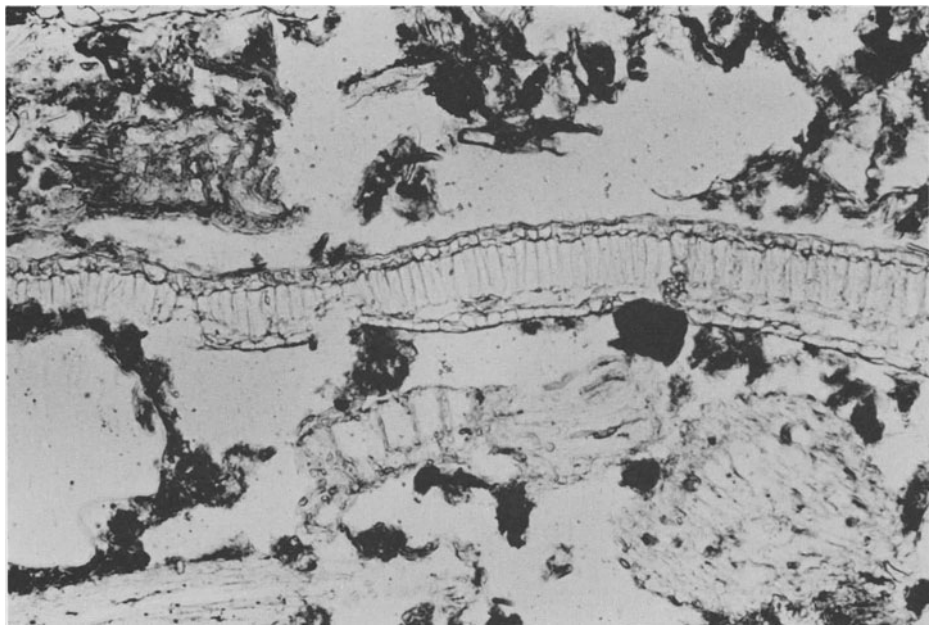

Figure 8. Leaf residues (occurring transversely), partly with unchanged leaf-browning substances (right part of the center leaf, piece of leaf below center), partly with darkened browning substances (top left), partly after decomposition of the browning substances and then still showing well the colorless unchanged cell walls (center). The very dark to opaque granular bodies on the leaves probably are collembola droppings (center below). Raw humus, F_m (Northwest Germany). Ground thin section (20 μm), bright field, natural size 380 μm.

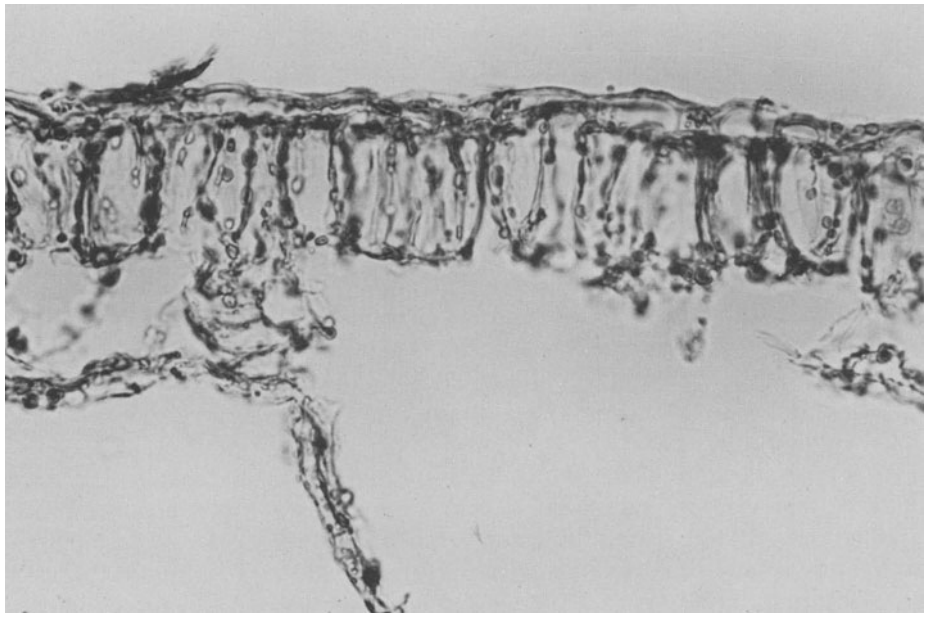

Figure 9. Beech leaf (cross section), L_v horizon. The nearly colorless upper cuticula is covered with dark substances; it separates from the epidermal outer wall (left). Epidermis and mesophyll are colored yellowish brown by leaf browning substances, which form in part very thin crusts in part conspicuous spherical bodies. Sponge parenchyma missing in some places. Lower epidermis broken up. Raw humus (Northwest Germany). Sliced section (20 μm), bright field, natural size 180 μm.

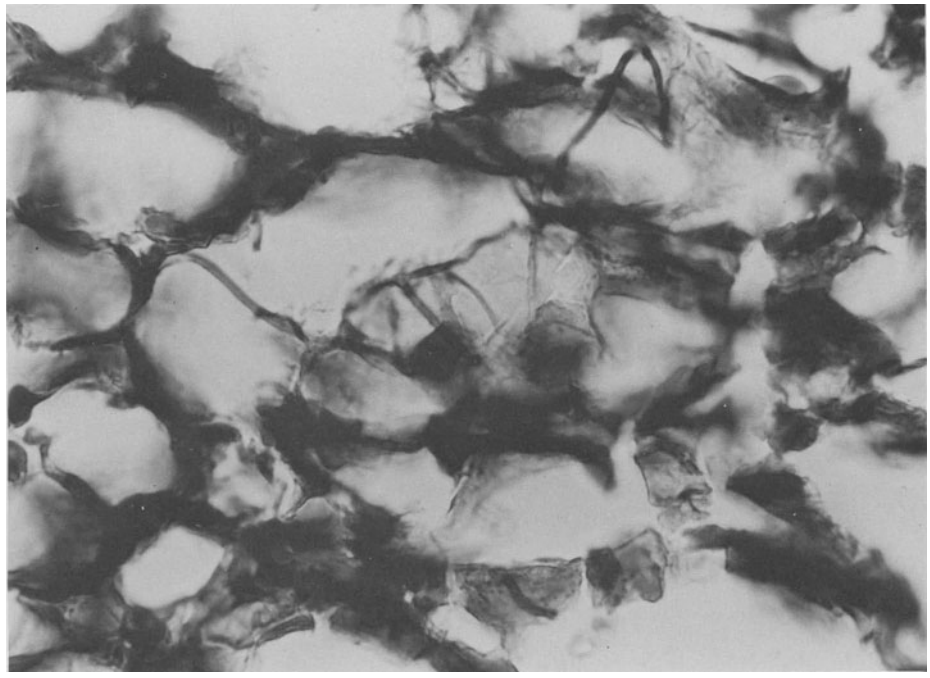

Figure 10. Leaf-browning substances in the assimilation parenchyma of an *Abies* needle. The cell walls are still well preserved (only partly torn), but on both sides irregularly encrusted by the browning substances. Shrinkage cracks in the browning substances. Some fungal hyphae. Moder, F_m (Black Forest, Germany). Sliced section (40μm), bright field, (strong green filter), natural size 180 μm.

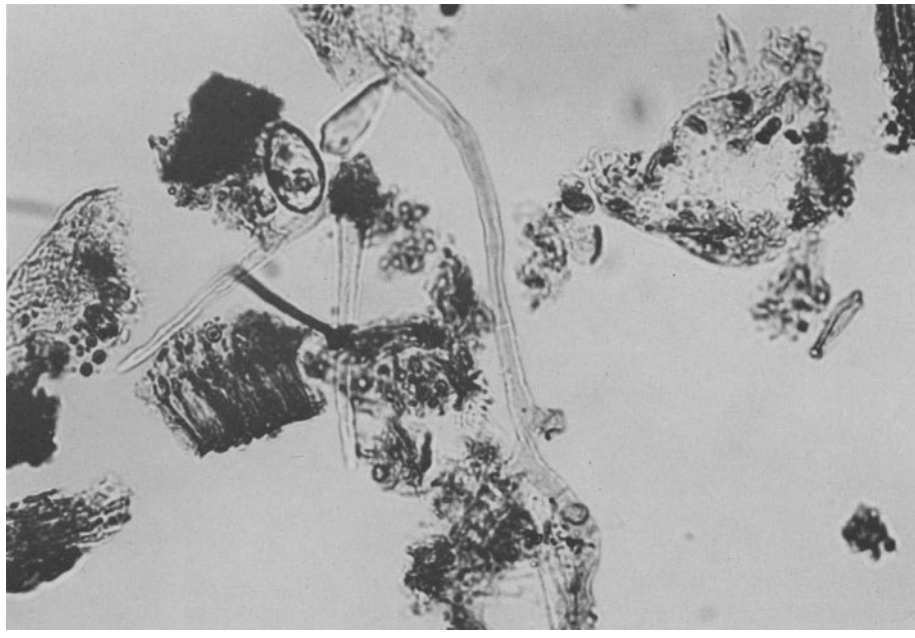

Figure 11. Debris preparation with fine substance particles of raw humus, F_m. Identifiable components, especially a thecamoeba shell (colorless, small, strongly contrasting oval, top left); double hair of a beech leaf (nearly colorless, immediately below); fragment of palisade parenchyma (strongly colored, below it); branched, septate fungal hypha (light brown, center); epidermis fragment (above right). Bright field, natural size 300 μm.

however, feebly colored parts were found, which appeared to have been formed from cell walls. Light refraction of these parts was greater than that of the unchanged cell walls (ALTEMÜLLER and BANSE [1964]). In partially decomposed Ericaceae roots and Sphagnum, a weaker cellulose reaction with iodine-potassium iodide and sulfuric acid was found (FRERCKS and PUFFE [1964]).

(β) *Microbiology* In ground thin sections of decomposing parenchyma, *fungal hyphae* can quite often be found (Figure 10). But even where this is not the case, the participation of fungal degradative processes cannot be excluded. Colorless or very thin hyphae are often very difficult to recognize in ground thin sections among strongly colored irregularly shaped degradation products (Section III C 2 c). In addition, the hyphae can exercise activity over distances of several cell diameters by the excretion of ectoenzymes. It is true that some authors disagree with this (compare Section III B 2 d γ). Finally the hyphae may be already decomposed at the time of investigation.

As an example of morphological observations on bacteria that have participated in parenchyma decomposition, the works of KONONOVA [1961] have already been cited. In the decomposition of root cortex, mycorrhizal fungi which have become parasitic can, under certain conditions, take part (SCHAEDE [1962], MEYER [1964]. First, they degrade the pectin of the middle lamella, leading to a maceration of the tissue. KAUNAT and BERNHARD [1969] found pectinolytic species of Bacillus and Actinomycetes in the rhizosphere. Pectin decomposers are also regularly found on fallen leaves (*e.g.*, *Pullularia pullulans* [WIERINGA, 1955]).

Fungi can also be observed as producers of brown pigments in the mesophyll of leaves. This applies especially to the congestive zones of mycelial growth. These can often be found between bleached and unbleached regions of the leaf blade and may be recognized even macroscopically as brownish-black demarcations. They are the result of extracellular fungal pigments (Figure 48).

The microbial degradation of the leaf-browning substances is the central point of interest in the microbiological phenomena in mesophyll decomposition. HANDLEY [1954], in numerous experiments with semisynthetic products and different fungi, established that the leaf-browning substances are, as a rule, difficult to degrade. But lignin-decomposing fungi seem to be capable of promoting this decomposition. This does not mean, however, that in bleached leaves the lignified tissues would likewise be already decomposed. It is true, however, that they are more decomposed than in brown leaves (BABEL [1972b]). FALCK [1930] observed a clearing of beech leaves by the white rot fungus *Agaricus nebularis*, and KÜHNELT [1963] by *Clitocybe infundibuliformis*. In natural mull and moder formations, MEYER [1962] found macroscopically visible white aerial mycelium of *Mycena sanguinolenta* between bleached beech leaves and *Picea* needles. For some other species, see LEHMANN, MEYER, and SCHONLAU [1969]. Some of these fungi, as well as other lignin-decomposers (LINDEBERG [1955]), were found by MÜLLERSTÄEL [1962] only on mull and closely related moder formations. This seems to be in agreement with an hypothesis of FALCK [1930] that the lack of lignin decomposers is essential for raw humus formation. However, MIKOLA [1956] found bleached leaves as well as lignin decomposers in raw humus. Such contradictory observations are not surprising, since a whole series of factors are responsible for the much-discussed differences between mull formation and raw humus formation (see also the following section).

(γ) *Chemistry* According to morphological results on the decomposition of cell walls, cellulose does not seem to be concerned directly in the neoformation of brown substances. It is probably mainly mineralized, but partly converted into microbial substance.

Of chief interest here is the mode of formation and the chemical nature of the leaf-browning substances. According to HANDLEY [1954], it involves the formation of tannin-protein complexes. The tannins in living cells are localized in the vacuole, the proteins in the

protoplast. On the death of the cell, the plasma membranes are broken down, and proteolytic enzymes and polyphenol oxidases are liberated from the protoplast. In addition, the redox potential of the cell increases. Polyphenolic tannins are thereby oxidized to quinones, which polymerize and, at the same time, take up amino acids released from the proteins. During these processes a color change—from no color to yellow and finally to brown—takes place. Chlorophyll may also be incorporated in the polymerisates, resulting in even a greater deepening of color (BÄBLER [1957]). Furthermore, an incorporation of monosaccharides into these mixed polymerisates is not improbable; for, according to NYKVIST [1963], monosaccharide-amino acid reactions in aqueous leaf extracts must be considered. Thus, purely autolytic postmortal processes lead to the formation of leaf-browning substances. They occur before decomposition of the cellulose walls begins. That means that extensively transformed as well as completely unchanged constituents exist in partially decayed plant residues. This is also indicated by absorption studies with fluorochromes (PAULI [1958, 1960]).

Differences in the quantity and stability of the tannin-protein complex in litter of different sites were found by HANDLEY [1954, 1961], COULSON *et al.* [1960a, b], and DAVIES *et al.* [1964a, b], and were thought to be responsible for the differences between mull and raw humus (see also DAVIES [1971]). Thus, the tannin content of beech leaves from a raw humus site was about 50% higher than of beech leaves from a mull site. In addition, typical raw humus plants, such as *Calluna*, are characterized by particularly high tannin contents (about twice as high as in beech). Finally, in weakly to strongly acid media, aqueous leaf extracts showed maximal precipitation action in gelatin solutions as well as maximal resistance of the precipitate to degradation by fungi.

In the degradation of leaf-browning substances by fungi, water-soluble tannins appear, and in addition, a fall in pH of about 2 units may be observed (KÜHNELT [1963], MIKOLA [1956]).

Apparently, leaf-browning substances are frequently falsely determined to be lignin by chemical analysis in the determination of lignin as an acid-insoluble residue. This explains the high lignin contents often given for litter (*e.g.*, birch litter 39% in comparison with pine wood 29%, (SCHEFFER and ULRICH [1960]). WITTICH [1943] found that a considerable proportion of the lignin fraction of needles in the litter in contrast to that in living needles was insoluble in acetyl bromide. This result might also be interpreted to be due to the formation of leaf-browning substances after the death of the needles and their erroneous inclusion in the lignin fraction. The same holds for the increase in nitrogen content of the lignin fraction, which is regularly found in the course of decomposition. GROSSKOPF [1935], even on the basis of morphological analyses, erroneously interpreted the leaf-browning substances as lignin degradation products, which were thought to have been produced in the decomposition of mesophyll cell walls. This interpretation was part of the basis for further discussions in the older humus literature (MAIWALD [1939]).

(c) Phlobaphene-Containing Tissues

(α) *Morphology* Many of the strongly colored "rotting products" often attract attention in sections of dystrophic or water-influenced humus forms (*e.g.*, of pseudogleys and gleys). They may be found on more precise morphological analysis to be residues of phlobaphene-containing tissues. The conspicuousness and wide distribution of such residues have even led to the separation and separate description of this group of tissues.

Their resistance to decomposition can be observed particularly well in fairly old cortex and cork tissue of roots. These tissues, as a rule, are preserved much longer than the central cylinder and inner parts of the cortex, which are formed from phlobaphene-free parenchyma (VAN DER DRIFT [1964]). The residues of cortex certainly show thereby a progressive loss of

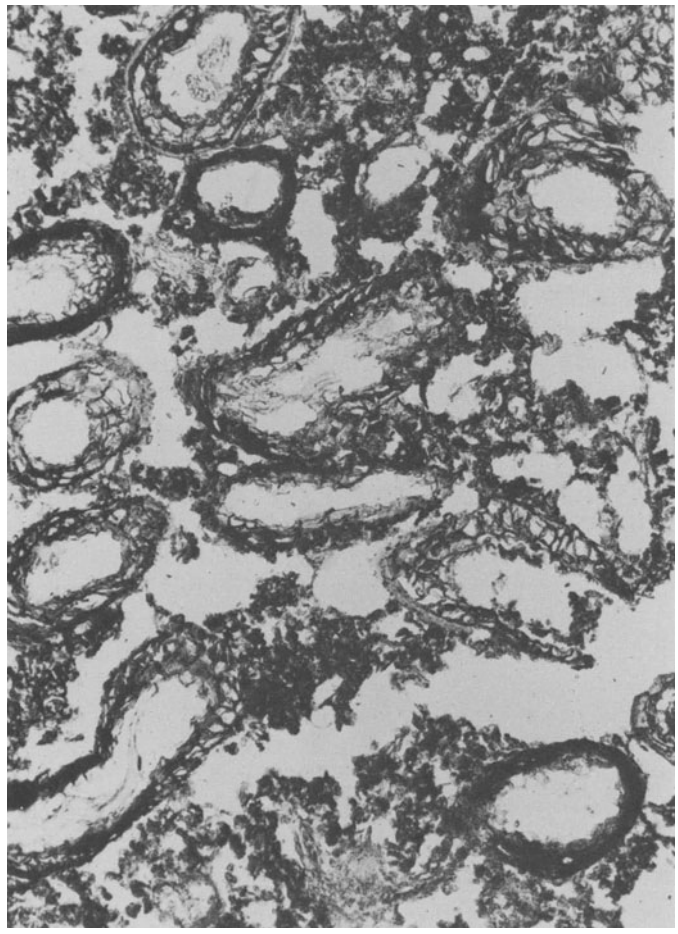

Figure 12. H layer, very rich in fine root residues. The central cylinders of the transversely or obliquely occurring root residues are partially or wholly decomposed, the cortex usually entirely preserved (partly collapsed) and colored reddish brown by phlobaphenes. Wet moder over peat, H horizon (Black Forest, Germany). Ground thin section (20 μm), bright field, natural size 1.5 mm.

the cell structures, but the color of the tissue remains unchanged for a long time (Figure 12). The residues of the cork tissue, which are cast off in the course of the thickening of the root are which originate from twigs, the wooden parts of which is decomposed, often accumulate in considerable quantities in the humus substance layer (Figure 43) (BABEL [1972b]). Particularly striking are the brownish-red cork residues of roots of the dwarf pine (*Pinus mugo*) in the tangel (Figure 13). On such residues a maceration often takes place which leads to the liberation of the individual cells, which then enter into the fine substance as intensely colored small bodies (Figure 15) (see also HOLLING [1958] and GROSSE-BRAUCKMANN [1963] (observations on residues of Ericaceae roots in peats). In peats and sometimes to some extent in other humus forms, even before the maceration, the phlobaphenes found in the cell lumen show an intense coloration, whereby the whole tissues may be finally transformed into coal-like masses (Figure 16) (HOLLING [1958], BABEL [1964b]). Fungal hyphae always seem to be present in this process. As yet, a complete disappearance of phlobaphenes, analogous to the disappearance of leaf-browning substances in the bleaching of leaves, does not seem to have been found anywhere.

JABLONSKI [1963], in decay experiments, noticed the appearance of fluorescent products in the vicinity of decomposing root cork. These products were found only at a certain intermediary stage of the decomposition.

Resistance to decomposition, similar to that of phlobaphene-containing tissues, is shown according to morphological observations, also by other outer tissues that are free of phlobaphenes but show suberinized cell walls. This pertains to some species of cork tissue as well as to exo- and endodermis of many roots. Where suberinization of the cell walls and phlobaphene content of the tissues coincide, as in the case of a normal tannin cork, the tissues that are most resistant to decomposition are formed. (For suberin, see also Section III B 2 e). Barks contain mostly phlobaphene, but they also contain some suberin tissue. ALLISON and KLEIN [1961] and ALLISON and MURPHY [1963] have shown that they decompose more slowly than wood.

(β) *Microbiology* It is well known that polyphenols, from which the phlobaphenes are formed, often exert an antibiotic effect (*e.g.*, WENZEL, KREUTZER, and ALCUBILLA [1970], who

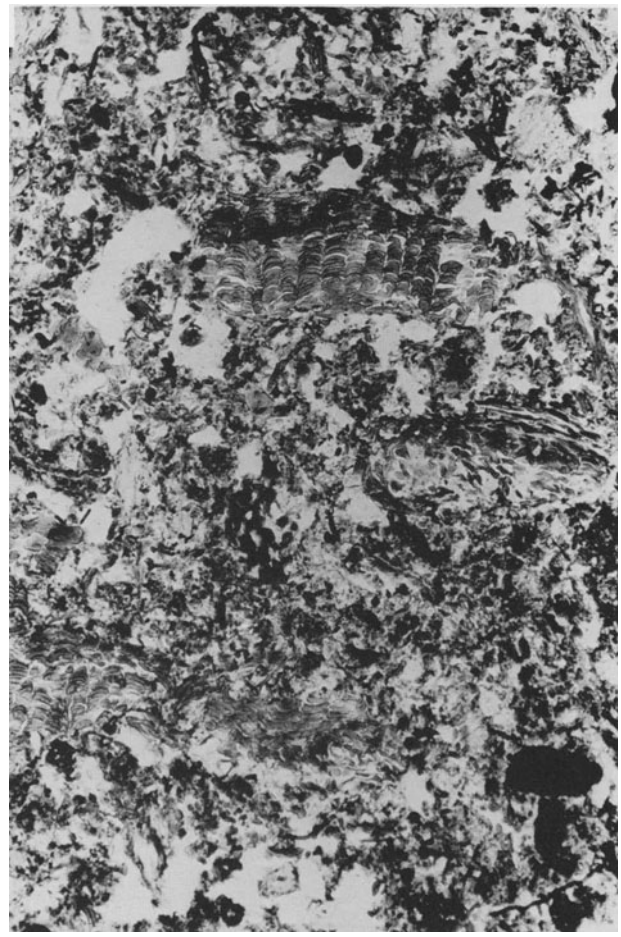

Figure 13. Brownish-red cork residues (mostly occurring transversely) of *Pinus mugo* in the H_r horizon of an oligotrophic tangel. Three larger cork residues are easily recognizable, some smaller ones are placed obliquely (*e.g.*, the black appearing in the center) Fairly dense fine substance: the black-appearing bodies, 5 to 10 μm in size, are single, reddish-brown cork cells (Alps). Ground thin section (15 μm), bright field, natural size 450 μm.

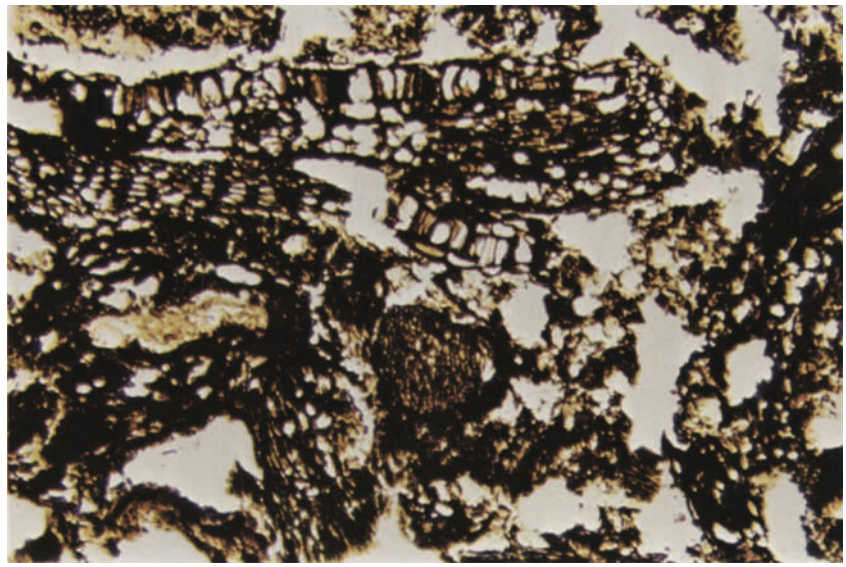

Figure 14. Uniform brownish black staining both of the plant residues as well as of the fine substance, probably by dissolved humus substances (thin parts appearing bright, thick parts opaque). Many leaf residues (transverse, center and top). Fossil (postglacial) wet moder of a heath (North Germany). Ground thin section (15 μm), bright field, natural size 450 μm.

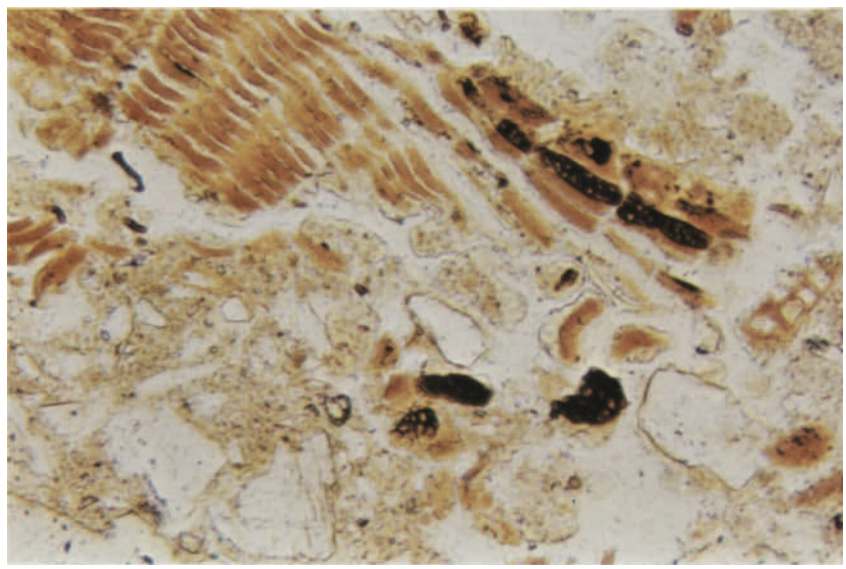

Figure 15. Cork tissue residues (transverse) in the mineral soil, cast off from root bark. The parts that are still coherent show the parallel row arrangement of cells characteristic of cork. Cell lumina reddish brown from phlobaphenes, cell walls colorless. Small groups and individual cells liberated by maceration. In places, cell contents transformed into dark fungal material. B/(B) horizon of a podzol-brown earth (Black Forest, Germany). Ground thin section (20 μm), bright field, natural size 350 μm.

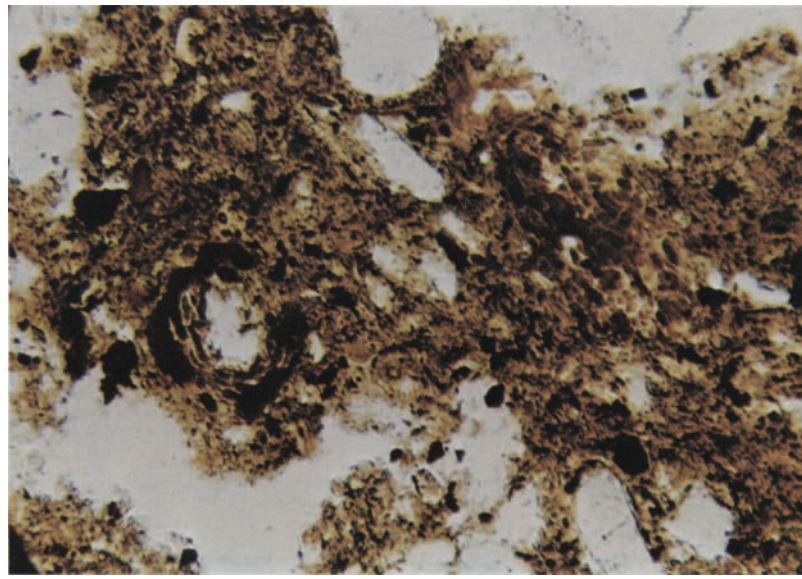

Figure 16. Two root cortices: right, oblique, without distinct outlines, brownish red; left, transverse, dark brown to opaque because of color change of the phlobaphenes (probably because of oxidative processes), central cylinder decomposed. Fine substance with high mineral content, some quartz. Wet moder with transition to peat formation. A_h (Black Forest, Germany). Ground thin section (25 μm), bright field, natural size, 0.5 mm.

investigated polyphenols from fir bast). The phlobaphenes themselves are difficult to degrade by microorganisms. Thus, phlobaphenes and the related monomers may protect from decomposition tissues which are impregnated by them. A maceration, however, may take place by pectinolytic microorganisms, as occur in the rhizosphere (*e.g.*, KAUNAT and BERNHARD [1969]).

Two cases of the blackening of phlobaphenes can be distinguished at moderate to fairly high magnification. The cell lumina can be densely filled with blackish-brown fungal mycelium (Figure 15). That means that the phlobaphenes are transformed into structural substances of fungi, mainly melanins and chitin. This is a parallel to the dense colonization of parenchyma cells by myxobacteria (KONONOVA [1961]), mentioned in the previous section. Under different conditions the phlobaphene bodies may darken with no other recognizable morphological changes occurring, but fungal hyphae are then often found on the surface of the tissue. In any case, probably only fungal groups such as basidiomycetes, which can also degrade lignin (HOLLING [1958], BABEL [1964a]), are capable of attacking phlobaphenes. According to BURGEFF [1961], catechin tannins of Ericaceae roots are degraded by the mycorrhiza-forming fungi.

(γ) *Chemistry* The formation of phlobaphenes shows a certain parallelism with the formation of the leaf-browning substances. In the degenerating metabolism, oxidases and peroxidases cause the oxidation and polymerization of monomeric tannins still in the living plant. Probably an incorporation of proteins is also involved therein (STAMM [1958]). Like the leaf-browning substances, phlobaphenes appear in the acid-insoluble residue designated as the lignin fraction (cf. Section III B 2 b γ) of substance groups analysis. The occasional blackening of phlobaphene-containing residues in the soil might indicate a higher oxidation.

From the morphological study of the decomposition of phlobaphene-containing tissues

it becomes apparent that the phlobaphenes, and the whole tissues as well, are highly resistant to degradation. Frequently observed maceration indicates only a degradation of the pectin.

(d) Lignified Tissues

(α) *Morphology* As has already been mentioned, lignified tissues are decomposed more slowly than parenchyma under generally favorable decomposition conditions. In raw humus, on the contrary, they are often decomposed more quickly than parenchyma. For example, HANDLEY [1954] has found that in raw humus the parenchyma of the medullary rays is often better preserved than the lignified parts of the wood. BABEL [1972b] found rather a fast-disappearing of lignified tissues from twigs and tree roots in moder.

In ground thin sections of soil, *charcoals* are frequently found. Where they occur in fairly large pieces, they show very well-maintained structures. When very thin, they are brown and translucent, but otherwise opaque. Very small pieces (from 5 to 30 μ), which are often encountered as opaque constituents in superficial humus forms, can be recognized as charcoal with some certainty on the basis of their sharp-edged, straight-faced outlines and their very slow decolorization with sodium hypochlorite (Figure 17). By treatment with sodium hypochlorite,

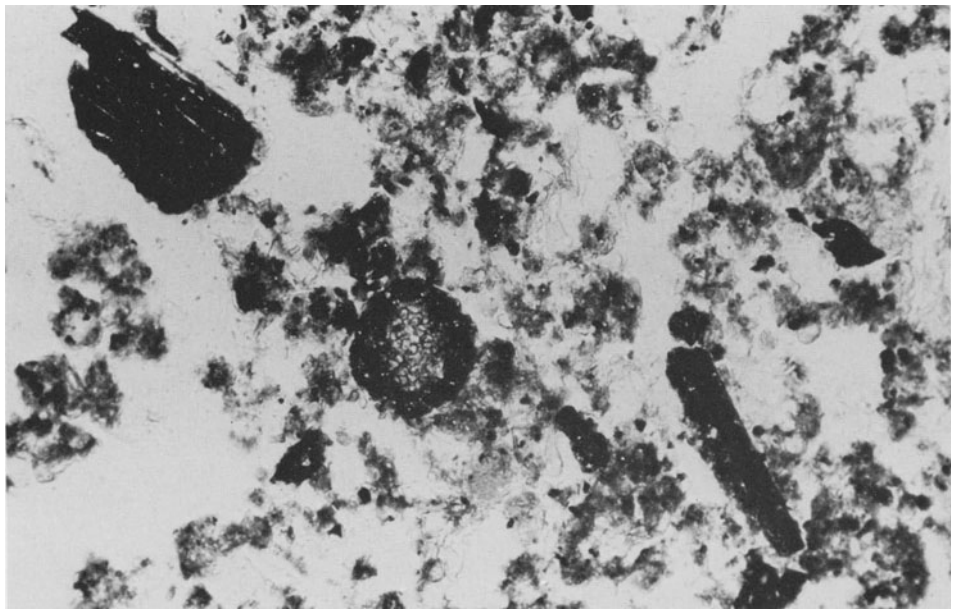

Figure 17. Two charcoal fragments, recognizable by their sharp-edged, in part parallel contours. A sclerotium (in the center). The very small, opaque particles probably are charcoals. Wet moder, A_h (central uplands of Germany). Ground thin section (15 μm), bright field, transmitted and incident light, natural size 450 μm.

which can also be carried out on ground thin sections, wood structures that previously were invisible because of the opacity of the particles become recognizable (BABEL [1964b, c]). Somewhat larger pieces of fossil charcoals may be determined taxonomically in the incident light microscope (MÜLLER-STOLL [1936], HOLDHEIDE [1941]). Details of structures, such as pits, remain well preserved. Only a slight shrinkage is liable to occur during carbonization. It is mainly in water-influenced humus forms that other plant residues also occur, even residues of leaves,

which are dark brown to black and more or less opaque but, at the same time, show tissue structures that are scarcely changed (see Part V B).

The decomposition of wood by fungi has been very well investigated on account of its technological significance (*e.g.*, BAVENDAMM, MÜLLER-STOLL, and VON PECHMANN in Freund, volume V/2 [1951], RYPACEK [1966]). Electron microscope studies are reported by MEIER [1955], RYPACEK [1960, 1966], LIESE and SCHMID [1962], LIESE [1964], and SCHMID and LIESE [1964].

The two main types of fungal decomposition are called *white and brown rot*, corresponding to the discoloration of the wood. The tissue remains intact for a very long time, even after severe rotting. The individual cell wall layers behave quite differently, however. The secondary wall is in most cases attacked first. The most resistant to decomposition are the primary wall, the tertiary wall, and the substance filling the spaces between the cells consisting of almost pure lignin.

Fungal hyphae in both types of rot are generally found only in the lumen of the cells. Often they are almost colorless and, therefore, in the unstained preparation escape cursory observation. Under the electron microscope, microhyphae can be detected which branch out from the hyphae in the cell lumen and penetrate the walls. They are only 0.1 to 0.4 μm thick (LIESE [1964]). The hyphae lying on the walls are often surrounded by a narrow zone (up to about 3 μm wide) of lysis. Furthermore, degradation patterns are found in the secondary wall, the orientation and rhombic shape of which correspond roughly to the fine structure of this wall layer. These changes can also be recognized under the light microscope as indentations and flaws.

In brown rot, decomposition is often unevenly advanced in patches. Places with more severe decomposition can be easily recognized under the light microscope with crossed polarizers: the birefringence of the cell walls has largely disappeared there, before severe morphological changes are detectable by transmitted light (Figures 18, 19) (KUBIENA [1943], VON PECHMANN [1951]). In the electron microscope, however, in this stage it may be seen that the cell walls show sponge-like porosity in the portions no longer birefringent. In advanced stages they can become thinner by collapsing.

These microscopic investigations correspond to the chemical results, according to which brown rot is mainly characterized by cellulose degradation. A porous lignin skeleton remains after loss of birefringence due to cellulose. New formations in the place of the cellulose are not found, if one disregards the occasional occurrence of residues of excretions or of humification products of fungi.

In the case of white rot the electron microscope reveals a loose structure of cellulose fibrils in the secondary wall. Later the secondary wall disappears completely; SCHMID and LIESE [1964] were able to establish therein a layer-by-layer degradation. In contrast to brown rot, the middle lamella is often more readily attacked than the secondary wall.

These observations show—again in harmony with the chemical results—that in the first stages white rot breaks down mainly lignin and in later stages also cellulose. Brown colorations, which were found in intermediary stages (MEIER [1955]), may probably be interpreted as degradation products of lignin. In later stages, however, as indicated simply by the white color even macroscopically, there are no colored degradation or transformation products.

The decomposition of lignified tissues in the soil was studied by BABEL [1964a], with the light microscope, in the sclerenchyma and xylem of beech leaf veins. The material had been isolated from a natural raw humus formation. As a rule, the secondary wall is attacked first, as in the decomposition processes just described. It becomes yellow. Then it is detached from the middle layer, becoming further discolored. Finally, when seen in cross-section, it forms a

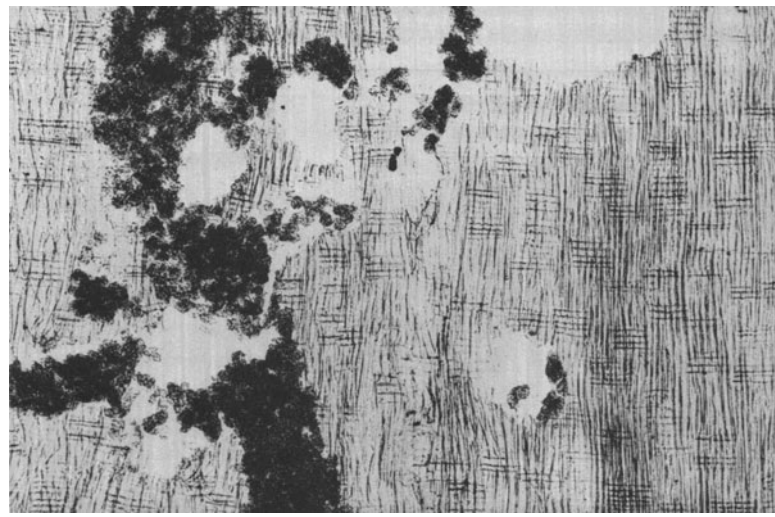

Figure 18. Brown rot *Pinus* wood, longitudinal section (cf. Figure 19). Tissues still intact (but stained yellow), apart from large feeding cavities, which are partly filled with droppings and decomposed dropping material. From moder (North Germany). Ground thin section (70 μm), bright field, natural size 1.5 mm.

Figure 19. Like Figure 18 but under crossed polarizers. The morphologically well-preserved tissue is strongly birefringent only in patches; in other patches the cellulose is largely degraded.

brown lump, which lies in the lumen of the still completely intact middle layer. In a final stage which, however, is not often found because the veins are usually consumed by animals before then, this lump has disappeared completely (Figure 5). In rarer cases, conversely, a discoloration and subsequent disappearance of the middle layers occurs before changes in the secondary wall are observed. In these investigations fungal hyphae were found within the tissues only occasionally.

As far as is known, the decomposition of lignified tissues of leaves of other tree species or

in other humus forms proceeds similarly (BABEL [1972b]). In mull, however, the formation of brown substances from the secondary wall is seldom found. In mull as well as in moder, the slightly lignified hypodermis of *Abies* needles formed only a few yellow decomposition products, which then disappeared without residues.

Woods that have decomposed under water show very similar morphology (MÜLLER-STOLL [1951]). The secondary wall in the cross section is transformed into rings and later to lumps. Ultimately, a homogeneous mass is formed from the whole cell material.

(β) *Histochemical and histophysical investigations* on the decomposition of lignified tissues in natural humus formations were made by BABEL [1964a]. The most important of the results are listed in Table 1, arranged according to the morphological decomposition stages of the secondary wall that have been outlined in the previous section.

For cellulose, birefringence was used as a qualitative criterion. For lignin detection, the blue primary fluorescence was used, as well as the absorption maximum at 280 nm and the phloroglucinol reaction. Sodium hypochlorite was used for the characterization of the newly formed substances.

Cellulose degradation is shown in Table 1 to run parallel to the morphological changes. The decrease in birefrigence indicates a destruction of the fine structure of the cellulose fibrils. From stage 3 onwards the morphologically unchanged middle layers can be stained with Ruthenium red. Since carboxyl groups are detected by Ruthenium red, this may be interpreted as the loosening of the fine structure or even as the incipient oxidation of the cellulose of the middle layer.

Lignin degradation begins at the side chains of the molecule, as shown by the early loss of the positive phloroglucinol reaction, which is specific for the side chains of the lignin units. Staining of the yellow and brown secondary wall residues with Schiff's reagent indicates the formation of aldehyde groups in the lignin degradation. Both observations are consistent with the results of macrochemical investigations (BRAUNS and BRAUNS [1960]). The absorption

Table 1. Morphological, histochemical, and histophysical investigations of beech leaf veins from a raw humus—degradation of the secondary walls in the sclerenchyma. (From BABEL [1964a]).

	1	2	3	4	(5)
Age	Fresh After $\frac{1}{2}$ year	After 1 year and later . . .			
Color	Colorless	Yellow	Brown-yellow	Yellow-brown	Sec. wall disappeared
Double refraction	+	+	(+)	(?)	
Fluorescence	+	+	(+)	(?)	
280 nm max.	+	(+)	(+)	—	
Phloroglucinol	+	?	—	—	
NaOCl	Not dissolved	Decolorized; partly dissolved		Decolorized; mainly dissolved	

maximum at 280 nm disappears after the loss of the positive phloroglucinol reaction. The specific lignin fluorescence disappears at last, and at about the same time as the birefringence. The fluorescent color seems to have been previously transformed to yellow. This effect, however, is due to the real color of the more strongly decomposed secondary wall (Figure 4). Accordingly, in the case investigated, simultaneous degradation of lignin and cellulose is involved (MEIER [1955]).

Decrease in the blue fluorescence of lignified tissues in the course of decomposition was observed also in straw by ALTEMÜLLER and BANSE [1964] and in lucerne roots by JABLONSKI [1963]. (For further details see Part VI B 3.)

Decolorization and solubility by sodium hypochlorite are properties which the secondary wall residues have in common with other brown humic substance materials, namely, the leaf-browning substances and the phlobaphenes already discussed. The transformation of lignin and the formation of humic substances can be followed still more closely by recording *ultraviolet absorption spectra of the microscopic preparation.* A publication on these investigations by the author is in preparation. The absorption spectrum of lignin is obtained in a pure form from fresh secondary walls. The above-described morphological transformation stages give progressively continuous transitions from the absorption spectrum of lignin to the nonspecific spectra of humic acids, which descend rather uniformly toward the longer wavelengths. Extractions of the secondary wall residues, which likewise were performed on the microscopic preparations, and subsequent repetition of the spectral determinations afforded no essential changes in the absorption. From this, together with the light microscopic investigations, it may be concluded that the conversion of the lignified cell walls to humic substances takes place without any deep-seated intermediate depolymerization of the lignin. It seems rather that oxidations, cleavage of monomers, and polymerization processes, in the sense of a formation of humic substances, take place on the lignin skeleton which is still little changed in its basic structure.

(γ) *Microbiology* The importance of fungi to the decomposition of lignified tissues emerges from the morphological observations on brown and white rotted woods. According to various culture experiments, however, there are also bacteria, especially those of the *Pseudomonas* group, that are able to degrade lignin (PREVOT *et al.* [1954], SORENSON [1962]). Up to now, however, it is not sure they can bring about a complete degradation of the lignin skeleton or peripheral changes only (HAIDER and SCHETTERS [1967]). Reliable indications on this subject have not yet been obtained from morphological investigations. The scarcity of fungal hyphae in the degradation of lignified tissue in the soil, however, could point in this direction (see also Section III B 2 b β). Dense colonization of slightly decomposed or undecomposed lignified tissues or of pure lignin preparations by myxobacteria was occasionally found by KONONOVA [1961] and JABLONSKI [1963].

The lytic zones around fungal hyphae indicate a certain remote effect of the fungal ectoenzymes. Another fact already mentioned is of interest here. The middle lamella or the secondary wall is decomposed before the tertiary wall, although the decomposition in question is caused by fungi that grow in the lumen of the wood cells. This leads to the conclusion that the enzymes diffuse rather extensively. The quoted observations on leaf veins and the degradation of leaf-browning substances in the mesophyll, in which hyphae are seldom found, suggest perhaps that the ectoenzymes diffuse through several cells. In this connection one should bear in mind the possibility that fungal hyphae, in later decomposition stages of the tissues, can be decomposed without leaving any trace, as may be often observed in the degradation of wood (BAVENDAMM [1951]). Lignin-degrading fungi are characterized by the formation of phenol oxidases (LINDEBERG [1955], HAIDER, LIM, and FLAIG [1964]). The most efficient lignin decomposers are Basidiomycetes, but in soil, lignin degrading is done also by Asco-

mycetes (HAIDER and DOMSCH [1969]). For lignin degradation see the section on leaf-browning substances (Section III B 2 b β), which show similarities to lignin not only in their analytical behavior but also in the microbiology of their decomposition.

(δ) *Chemistry* As suggested by the morphological findings, the resistance of lignin to degradation is not so high as is often assumed from chemical analysis (see Part III C 3). When specific reactions for quantitative determination of lignin are employed, however, they give results that correspond to the morphological findings. KICKUTH *et al.* [1969] found only traces of lignin in the A_h horizons of mull and mull-moder intergrades, but cellulose in amounts of 7 to 11 % of organic matter.

From the morphology of the decomposition of lignified tissues, conclusions may be drawn about the role of cellulose and lignin as parent materials for the production of humic substances. The topochemical neoformation of humic substances at the site of degradation of cellulose and lignin can be observed in many instances, as pointed out above. Participation of cellulose degradation products in the formation of brown substances is not unequivocally clear, however, from these investigations. The major part of the cellulose is evidently mineralized (compare Section III B 2 e). The lignin degradation, similarly, often leads to a direct mineralization by white rot (SCHEFFER and ULRICH [1960]), but often also to the formation of brown substances, which in soil may be transformed further to stable humic substances, especially by reaction with ammonia or amino compounds. This is also supported by chemical degradation experiments on humic substances. Vanillin and closely related compounds can be produced from lignin by chemical degradation. According to JAKAB *et al.* [1962], they can be "cleaved from those parts of the humic substance molecules that still bear characteristics of lignin, in which case one considers at least a partial formation of humic substances through peripheral changes of lignins" (see also GRABBE and HAIDER [1971].) This is the same idea of the humification products of lignin as was deduced above from histophysical investigations. Moreover, chemical investigations show that in the microbial degradation of natural lignin fission products the same intermediates are formed (*e.g.*, hydroxy-*p*-benzoquinone) as occur in the preparation of model humic acids from hydroquinone (FLAIG, SALFELD, and HAIDER [1963]). According to GADD [1957], vanillin is oxidized in the presence of fungal ectoenzymes (laccase) to catechol and *o*-benzoquinone, and these compounds can then polymerize to brown substances. When incorporation of nitrogen is not possible, however, the polymerizates can be degraded anew by the fungi as far as mineralization (HAIDER [1965]). This case might be realized in the quoted intermediary occurrence of brown substances in white rots and also in the case of the disappearance of brown substances in beech leaf veins.

The formation of *lignin-protein complexes* (WAKSMAN [1936]) in the conversion of lignin to humic substances is not very likely, according to morphological investigations. This formation could begin only after the mechanical disintegration of the lignified tissues, followed by intimate mixing with residues of proteinaceous tissues. The lignified tissues are largely free of protein and also do not contain any significant amounts of microorganisms which, on autolysis, might be possible sources of protein. The lignin-protein complex might be largely identical with the tannin-protein complex discussed in Section b.

(e) Other Tissues

The cell contents and the side and inner walls of the *epidermis* behave on decomposition like parenchyma. However, the thickened outer wall and the cuticula deposited on it deserve special consideration. Both often remain intact for a long time. As the thin section observations show, they are not readily consumed by the smaller soil animals and they are attacked by microbes only with difficulty (Figures 33, 22, 6) (PUFFE and GROSSE-BRAUCKMANN [1963] and (GROSSE-BRAUCKMANN and PUFFE [1964]). With more strongly decomposed leaf residues

the cuticula (here understood in the broader sense—cuticula and cuticular layer) becomes wavy and cracked and, in places, separates from the epidermal outer wall. The histochemical and histophysical features investigated do not alter during these changes (observations on beech leaves by the author) (Figure 9).

The high resistance to decomposition of the epidermal outer wall with its deposits is due to the cutin. The resistance to decomposition of the cuticula on dead plant residues is consistent with its function in the living plant, to which it offers protection against pathogens (MADER [1958a]). In soils, however, there exist quite a lot of microorganisms which produce cutinase, as has been detected by HEINEN and DE VRIES [1966].

The exodermis of roots, which remains intact often longer than the primary cortex (see also KONONOVA [1961]), behaves similarly to the epidermis. Its resistance is caused by the suberin content of the walls.

Suberin and cutin, occurring on the cell wall as incrustations, are very similar to each other. They are essentially highly polymerized derivatives of fatty acids, but details of their composition are not yet precisely known. Sporopollenin, which forms the exin of pollen, is related to them. The degree of polymerization increases from suberin to cutin to sporopollenin. The resistance to decomposition appears to increase in the same order. Sporopollenin is the most resistant substance in the plant kingdom (see Section III C 2 c).

Collenchyma often is decomposed very quickly. Sometimes, however, masses of yellow-colored substances and, simultaneously, warty granular deformations of the inner wall parts may be observed (Figure 5), from a leaf vein. As a rule, the whole tissues disappear later

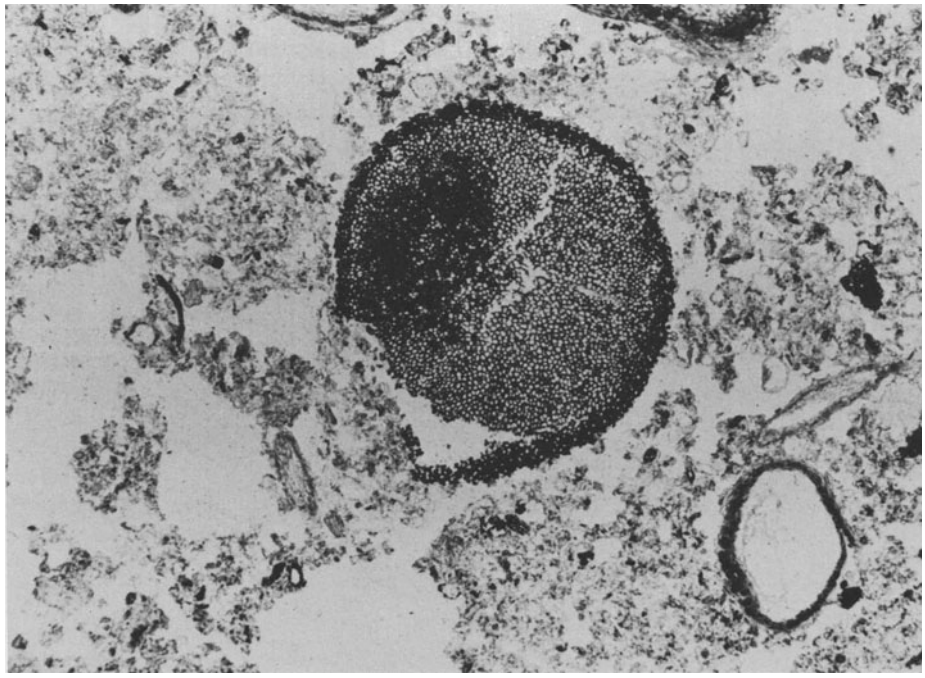

Figure 20. Sclerotium. The cortex can be easily recognized; it is rich in fungal pigments. The lower part is broken. In addition numerous small opaque particles, some of them are sclerotium fragments (*e.g.*, quite at the right). Below at the right a root residue, cork tissue still preserved. Raw humus, H (central uplands of Germany). Ground thin section (5 μm), bright field, strong blue-green filter, natural size 1.5 mm.

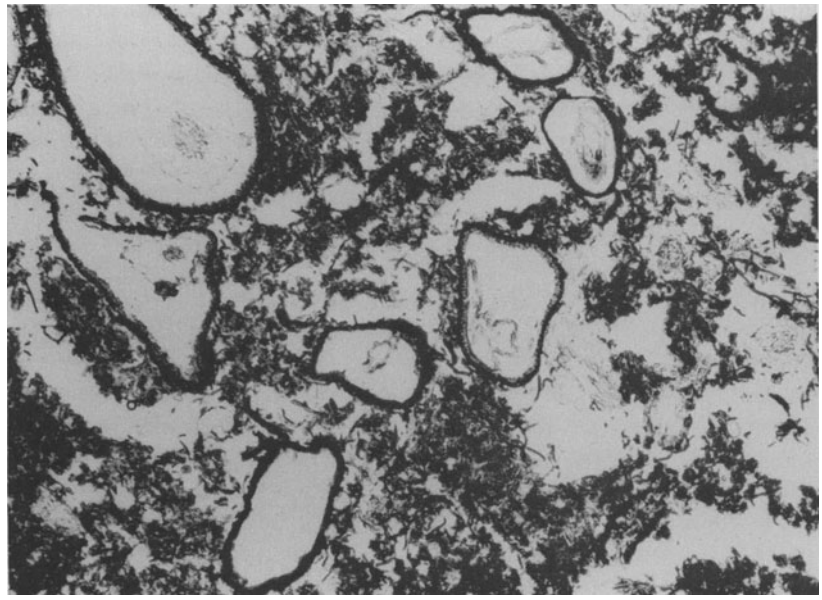

Figure 21. H horizon, very rich in fungal hyphae and hyphal residues. Mycorrhiza mantles as irregular dark rings; from these emerge hyphae, which together with hyphal residues constitute more than half of the fine substance. Only a few root residues are retained in the mycorrhiza mantles. Wet moder (Northwest Germany). Ground thin section (12 μm), bright field, natural size 1.5 mm.

without a trace (BABEL [1964a]). The relative ease of decomposition is induced by the looser structure and the high pectin content of the cell walls. If polyphenols play a role in the production of the yellow substances is not known. Otherwise, the discoloration should be taken as an indication of the production of colored substances from aliphatic compounds.

The *phloem* of the vascular bundles and the sieve strands of the bast are certainly the most easily decomposed tissues. In the upper litter layer, holes that are formed by the collapse of the *phloem* appear in the vascular bundles of leaves. The *phloem* residues form dense yellow masses with scarcely any structure. They disappear completely in the lower litter layer (BABEL [1964a], KONONOVA [1961]). This rapid decomposition is consistent with the thin-walled character of the sieve tubes and the phloem parenchyma cells and with the large proportion of pectin and hemicelluloses, especially callose, in the structure of the cells walls. Whether the disappearance of the phloem residues is due to removal in solution or to complete mineralization is not known.

The *fungal pseudotissues* of the sclerotias and mycorrhiza mantles are decomposed only with great difficulty (Figure 20). This is shown particularly clearly with mycorrhiza mantles, which often remain behind as nearly empty shells, while the roots surrounded by them are already decomposed (Figure 21). This resistance to decomposition might be largely due to fungal pigments. Their humic substance-like properties have been known for a long time. On the contrary, chitin, which is not impregnated with melanin, can be decomposed relatively easily (Section III C 3).

C. Organic Fine Substance

The small fragments which arise from the disintegration of plant residues, are called organic fine substance. In addition, under the morphologically collective group of the organic

fine substance are included other small constituents such as fungal hyphae and spores, pollen grains and newly formed bodies from the solution phase. This discussion refers particularly to the organic fine substance of moder and raw humus. In these cases the organic fine substance is quantitatively prominent and it is horizon-forming in the humus substance layer (Figures 25, 23, 22). Very similar is the organic fine substance of the upper part of the A_h horizon of moder and mull-like moder (Figure 26). (For information on organic fine substance in mineral soil, see Section D 2 b.)

1. *Mechanical Disintegration of the Plant Residues*

In the disintegration of plant residues, soil zoological as well as microbiological and non-biological processes are active. The kind of disintegration that predominates differs markedly in the different horizons and different humus forms.

The feeble disintegration phenomena in the L layer are attributable mainly to non-biological processes. Because of the marked change between moistening and drying out, swelling and shrinking stresses occur. Also the brittleness of many dry plant residues facilitates mechanical disintegration. On the contrary, disintegration by the feeding activity of animals in the L layer is small. However, in the F layer this becomes dominant. The activity of fungi also contributes to the disintegration of the plant residues in the F layer. It can outweigh the disintegration by animals in raw humus. In the H layer a further reduction in size of the particles is not morphologically immediately apparent, although the mineralization and solution processes that take place there do in fact work in this direction.

(a) Disintegration by the Activity of Animals

Most soil animals consume preferentially the softer and more hydrated plant parts. They are preferred because they are more palatable and because they contain microorganisms. The preliminary microbial decomposition of the plant residues and the microorganisms themselves provide an important source of food for soil animals (*e.g.*, ZACHARIAE [1965]). FÜHRER [1961] was able to show that dead Artemisia roots are preferred by an oribatid species to other plant residues because these roots were colonized by certain bacteria. For the nutrition of soil animals, see the summarizing accounts on soil zoology (*e.g.*, KÜHNELT [1961] and DUNGER [1964]).

By the selective uptake of food, there is formed, *e.g.*, the typical skeletonization of leaves, in which only the network of leaf veins remains intact (see also Section III B 2 a). That is chiefly the work of diptera larvae, diplopods, and larger oribatids, and less frequently of small arthropods. Earthworms also have similar feeding habits (EDWARDS and HEATH [1963]). Pieces of the leaf veins and leaf stalks remain behind.

The disintegration activity of soil animals becomes obvious also by analysis of their gut contents or excrements. The latter usually are called "Losungen" (droppings) in the German

Table 2. Bite sizes of soil animals. (After DUNGER [1963].)

Animal group	Bite sizes of the species examined
Diplopods	350–1000 μm
Isopods	250– 400 μm
Diptera larvae	400– 600 μm
Collembola	40– 170 μm
Lumbricidae	800–8500 μm

written micromorphological literature, fecal pellets in the English written literature. They are an important feature of the fabric of most humus soil horizons. Their size, shape, and arrangement, therefore, are dealt with in Part IV A 3.

The size of the tissue and cell fragments, which may be recognized in droppings, corresponds to the *bite size* of the soil animals. DUNGER [1963], by measurements of the fore gut content, has determined the bite sizes for the most important groups of litter-decomposing soil animals (see Table 2). The animals investigated had been recently caught in their natural habitat.

In the same work the hind gut contents were analyzed. In all the animal groups mentioned, several kinds of leaf residues were found, namely, parts of the vascular tissue and parts of the mesophyll and of epidermis, in addition to pieces of fungal hyphae and wood (the latter not in diptera larvae). Similar results to Dunger's were obtained by SCHUSTER [1956] (see also KÜHNELT [1961]) in very exact microscopic analyses of mite droppings. In these, animal residues (*e.g.*, chitin hairs), algal threads, and moss residues were also found. MACMILLAN and HEALEY [1971] have analyzed the gut contents of collembola.

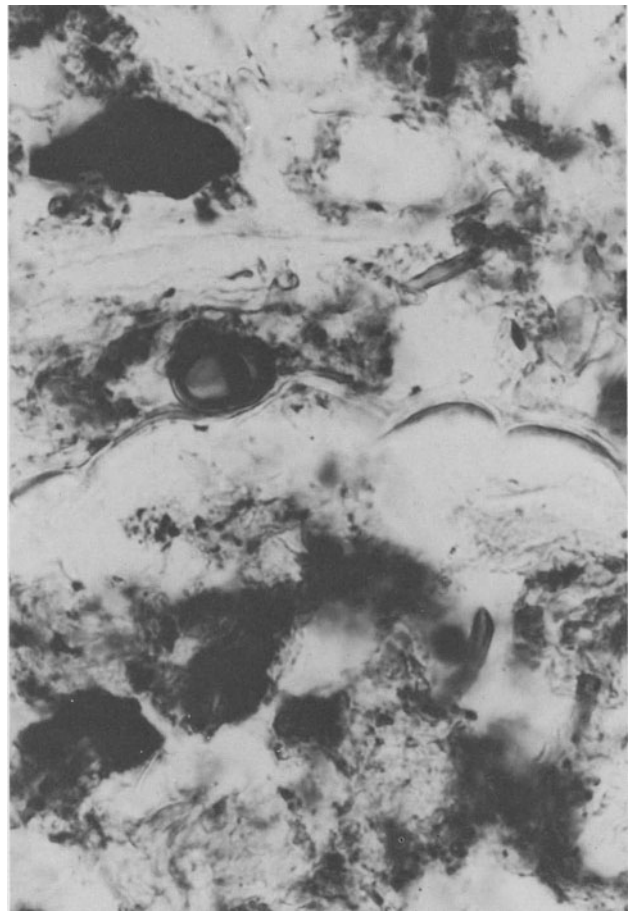

Figure 22. F_r horizon of a raw humus. Outer wall of a beech leaf epidermis well-preserved (horizontal band in the middle). Fine substance strongly differentiated by color. A fungal spore (left center) and some pieces of colored hyphae. (Northwest Germany). Ground thin section (20 μm), bright field, natural size 110 μm.

Morphological changes that shed light on essential chemical changes, such as loss of structure, color changes, or a distinct decrease in certain components of the food, cannot be found in fresh droppings (Figures 34, 48). This appears to hold for earthworm droppings also. There are two ecological groups of animals: Primary decomposers, which consume plant residues; secondary decomposers, which consume droppings of other animals. Both groups bring about mainly a disintegration of the organic matter. ZACHARIAE [1965] assumes that many litter-feeding arthropods utilize only the slime of microorganisms and the degradation products produced from them. Droppings, which consist of more strongly decomposed material, are always derived from more strongly predecomposed food, as indicated in the above-mentioned investigations of DUNGER [1963].

Comparative measurements on extracts of soil animals food with extracts of their droppings showed only non-uniform feeble color changes (DUNGER [1963]). A small rise in nitrogen content in the droppings and a slight loss of substance, which were largely attributable to respiration of carbohydrates (BIWER [1961)], were not expressed morphologically.

Old droppings, on the contrary, in comparison with fresh ones show a deepening of color which corresponds macroscopically to the color intensification from the F to the H layer. It indicates chemical changes in the dropping material *after* deposition. In investigations of west European podsols a darkening of droppings has been found, especially under dry or very wet conditions (RIGHI [1969]).

(b) Disintegration by Other Processes

After the decomposing action of fungi certain decomposition-resistant tissue parts often still remain. These disintegrate either as a result of mechanical stresses, such as swelling or shrinking, which always occur in the soil within small areas, or the parts remaining after fungal decomposition may be so finely divided that they are morphologically considered to be fine substance. An example of the latter case is the liberation of cells from the tissue association that is brought about by dissolution of the middle lamella (Figure 15). Detailed descriptions of disintegration by the decomposing activity of fungi are lacking in the literature.

The *mechanical disintegration procceses* due to alternate wetting and drying can be nicely observed especially on leaves. In the leaves of the L layer stresses occur between the lower epidermis and the vein network, which lead to a breaking up of the epidermis above the intercostal areas and finally to the liberation of small pieces of epidermis (Figure 9) (ZACHARIAE [1963]). Similar conditions cause the breaking up and breaking away of the lower parts of the leaf veins; these consist largely of collenchyma which, on wetting, swell more than the lignified parts of the leaf veins. Such processes, which are due generally to mechanical inhomogeneities and to swelling differences in the various tissues, are enhanced by partial microbial or animal decomposition.

The breaking up and piece-by-piece casting off of the root bark, which is a consequence of secondary thickening of the roots, leads similarly to the formation of small fragments of plant parts (Figure 15).

2. *The Constituents of the Fine Substance*

For detailed morphological analyses of the fine substance it is most convenient to work not with sections but with debris preparations, which are prepared from suspensions (see Part VI A 3 c). When necessary, the inner structures of strongly colored pieces can be made visible by decolorization with sodium hypochlorite. Application of fluorescence microscopy sometimes helps in the microscopic analysis of organic fine substance (see Part VI B 3a).

(a) Morphologically Identifiable Tissue Residues

Often among the conspicuous elements of the fine substance are reddish-brown homo-

geneous particles, spherical or longitudinal, about 20 to 40 μm in size. These are slightly deformed cells, which are released from phlobaphene-containing bark tissues and cork tissues by maceration. Still coherent groups of a few such cells also occur (Figures 15, 25, 13).

In debris preparations, moreover, very tiny pieces of the different parts of leaves can be recognized (see Table 3 and Figure 11). Easily recognizable in the example quoted were leaf

Table 3. Pieces of leaf in the fine substance of a beech raw humus.

Horizon*	Hairs	Pieces of			
		Cuticula	Epidermis	Mesophyll	Leaf veins
L_n	1–2	2–3	1	0–1	1
L_v	0 (–1)	2–3	2–3	1–2	1–2
F_r	0	x	3	5	1–2
F_m	0	x	1–2	5	4–5
H_r	0	x	0–1	3	3–4
H_f	0	x	x	3, x	2

Fine substance obtained with a 200 μm sieve; examination of debris preparations after sodium hypochlorite treatment. Estimation of the proportions in fine substance: 1 — rare; 5 — very frequent; x — hardly recognizable by purely morphological investigation. Investigations by the author. * = Symbols of horizons according to Babel [1971a] (see Section II C).

hairs, pieces of epidermis, the palisade parenchyma, and pieces of the leaf veins. Difficult to recognize were the colorless, irregular, thin, membranous pieces of the cuticula.

Table 3 shows the course of disintegration processes in the profile, which begins with the sloughing off of the cuticula already in the L_n horizon and ends with the disintegration of the leaf veins in the F_m horizon. The table shows also how, with increasing depth in the profile and therefore increasing transformation of the fine substance, these residues become increasingly difficult to recognize. For histochemical investigation of these particles, see Part III C 3. Pieces of soil animals, mainly chitin armour, may be found occasionally in debris preparations.

Corresponding investigations were performed in other cases, not on the total fine substance but on droppings or on the hind-gut contents of soil animals. The pertinent publications of SCHUSTER [1956] and DUNGER [1963] have already been discussed in Section III C 1 a. MÜLLER [1887] found in earthworm droppings pieces of moss leaves, beech leaves, and roots as well as hyphae.

(b) Morphologically Fully Destroyed Material

With increasing depth in the humus profile, an increasing proportion of the fine substance is changed so much that even on careful investigation only a strongly colored material with irregular structures may be recognized. In the F horizon this material, on microscopical examination, often shows bright colors, which in the H horizon recede in favor of darker and especially duller colors, and finally disappear altogether. Very dark to almost opaque parts, which often show granular internal structures, occur in different moder forms, particularly in the rendzina moder.

No clear features of the parent tissues can be recognized. The term "amorphous," however, which is often given to this material—particularly in the case of investigation at weak or medium magnifications—should certainly be avoided. Firstly, irregular structures can always

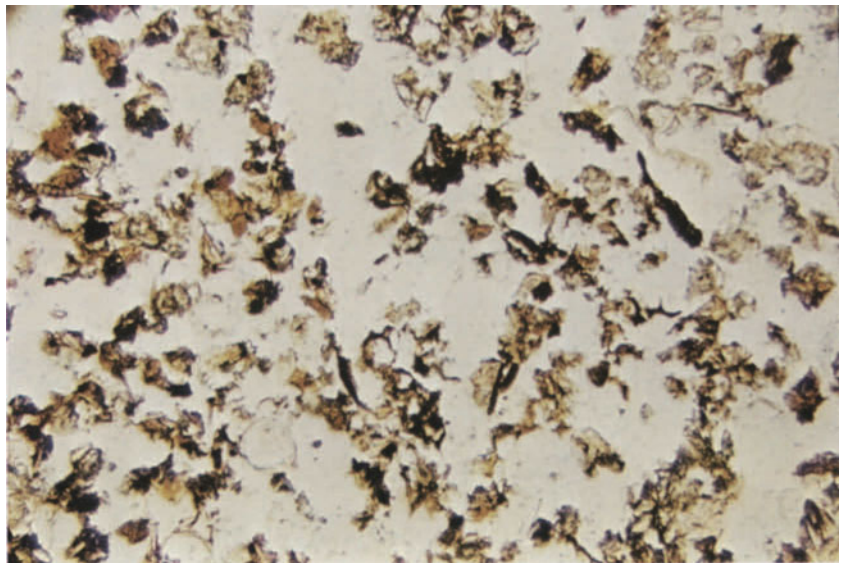

Figure 23. H/A_{hh} of a moder (detail of Figure 39, see Figure 24 (fluorescence) and 27 (crossed polarizers)). The organic fine substance particles allow traces of cell wall structures to be recognized at best indistinctly; mainly dull and dark colors. A few brown hyphae. Bright field, natural size 600 μm.

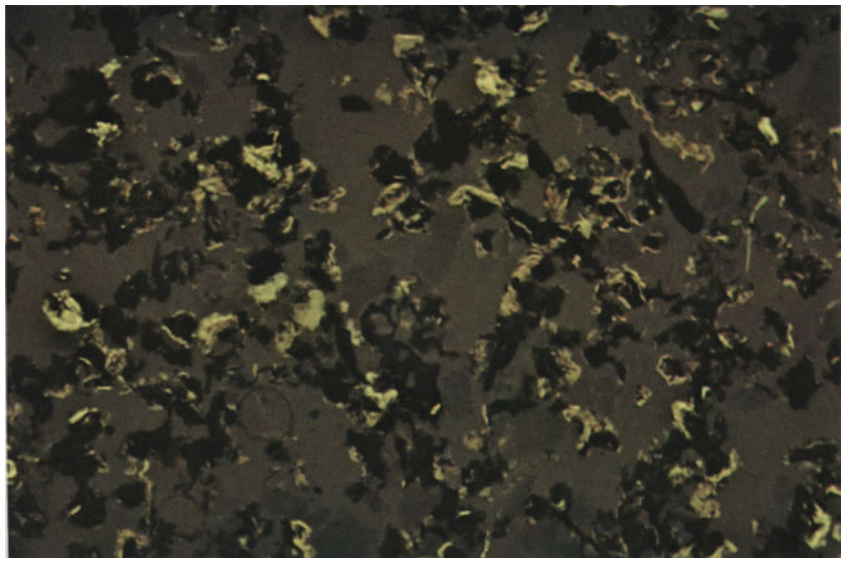

Figure 24. Like Figure 23 but with fluorescence illumination. Numerous cell wall residues visible by yellowish or greenish primary fluorescence, some of them colorless in bright field. Fluorescence color frequently impaired by substances that are brown in bright field.

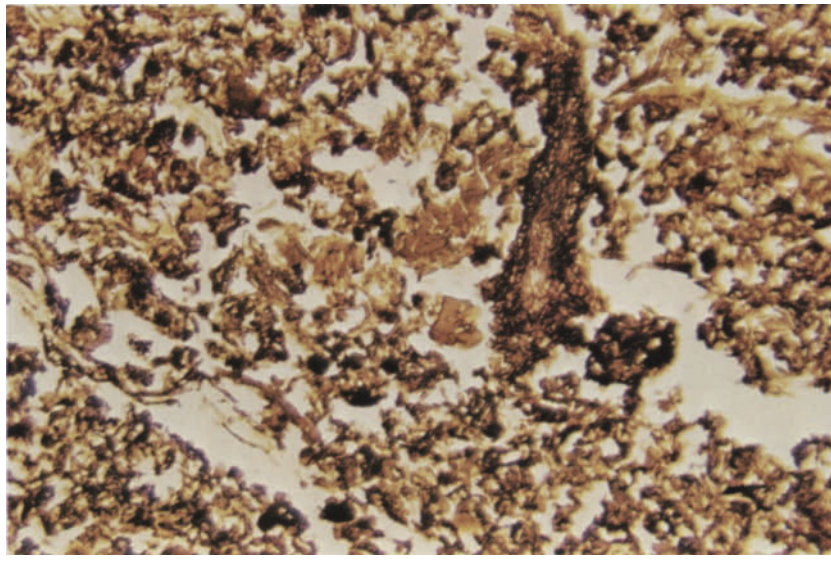

Figure 25. H_f horizon of an alpine pitch moder (dense fine substance fabric, detail of Figure 41). Small, brightly colored, cell and tissue residues sporadically recognizable (center, immediately to the left of the root). Many hyphae and hyphal residues. A root, running perpendicular, occurring mainly in the mycorrhiza mantle. Bright field, natural size 450 μm.

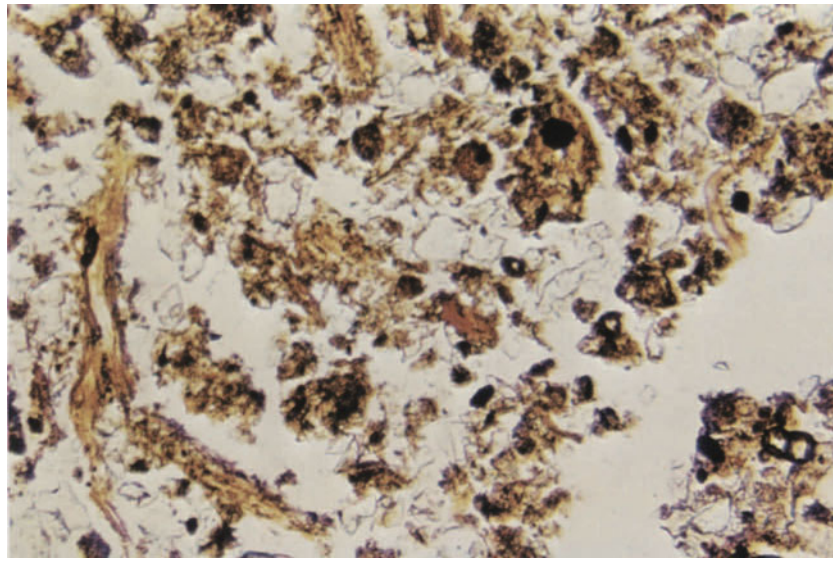

Figure 26. Mull-like rendzina moder, A_h horizon (detail of Figure 52, 53). The colored particles are organic fine substance; some yellowish brown, small tissue residues; left, a fine root. The colorless grains are calcite. (Vienna woods, Austria). Ground thin section (20 μm), bright field, natural size 450 μm.

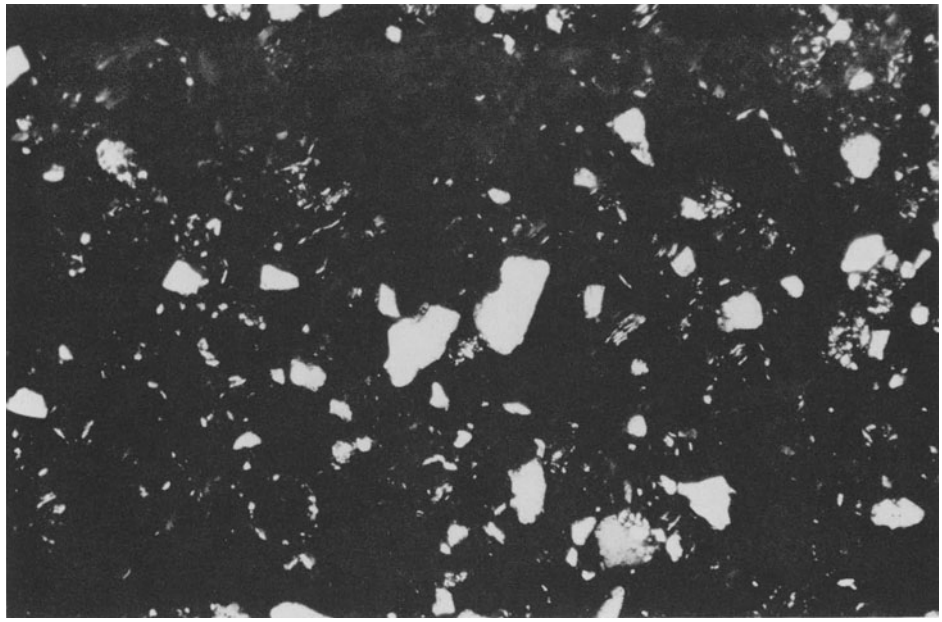

Figure 27. H/A_{hh} horizon of a moder under crossed polarizers (compare Figure 23 and 24). Quartz grains are visible because of birefringence; in addition organic parts (cell wall residues), which are sometimes not clearly distinguishable from small quartz grains. (Northwest Germany). Ground thin section (20 μm), natural size 600 μm.

be seen. Secondly, after treatment with sodium hypochlorite, it becomes evident that the material contains a large amount of cell wall fragments. These are coated with irregular, colored substances that are dissolved by sodium hypochlorite. In the fluorescence microscope the cell wall fragments may be recognized by their yellow and green or sometimes blue fluorescence, even without treatment with sodium hypochlorite (BABEL [1972a]). They are partly birefringent. The birefringence is, however, only very feebly apparent because of encrustation with colored substances. (Figures 24, 27, 23; see Section III C 3.)

(c) Microorganisms and Their Residues; Pollen

Microorganisms are discussed only briefly here, as far as they can be recognized as morphological elements in microscopic humus preparations.

Colored hyphae and spores of fungi may often be found in thin sections as constituents of the fine substance (Figures 25, 22). Frequently their characteristic dark brown with slight violet color helps in their recognition. Colored hyphae are widespread, especially in organic layer formations. The colored substances, which are similar to melanin and humic substances (see Part III C 3), occur in the fungal cell walls, to lower amounts also in the cytoplasma. They can be formed also on the surface of the cell walls (sometimes in a mucilage layer, photo in DOMMERGUES and MANGENOT [1970]).

The study of fungal hyphae as constituents of soil organic matter is of interest for two reasons. On the one hand, fungi participate decisively in the degradation of plant residues; on the other, the dead residues of fungi are in turn a component of humus.

Hyphae are found in and on the plant residues, as well as in the pores (*e.g.*, Figures 10, 32). On mineral particles they occur to a much lesser extent (indirect studies in a podzol by

WILLIAMS and PARKINSON [1964]). In 1932 KUBIENA had already investigated the positions of fungi in the soil pores with the incident light microscope (KUBIENA [1932, 1938, 1943a]). Chewed pieces of hyphae often occur in droppings of mites and other soil animals (Figure 35) (DUNGER [1963]). Mycelial strands are sometimes found in moder and raw humus. They may be observed more easily under the stereomicroscope than in ground thin sections. Fungal hyphae, which are present for the most part in small fragments, can be found in abundance in the H layer of wet surface humus formations (ROMELL [1935] in greasy mor). In such cases it may often be morphologically established that the hyphae emerge from mycorrhiza mantles (Figures 28, 21). MEYER [1964] found the same in the upper F horizon of dry raw humus formations.

Colorless hyphae are easily overlooked in thin sections. Therefore, NICHOLAS and PARKINSON [1967] judged ground thin sections to be not quite suited for quantitative assessment of fungal mycelium. With phase contrast illumination, however, they may be found unequivocally in sufficiently thin sections (ALTEMÜLLER and BANSE [1964]; observations of the author). They are often filled with air and thereby more easily visible, but they may also be compressed. Colorless hyphae sometimes become visible in sections through their strong primary fluorescence (Figure 28; JABLONSKI [1963]). They are much less frequent than the brown hyphae, a fact that is quite in harmony with their experimentally established more rapid decomposition (see Section III C 3). Sometimes autolysis of hyphae may be observed, as well as lysis after colonization of bacteria (BURGES and RAW [1967]). On the average fungal hyphae in soil are thinner than in nutrition media (ZVAJGINCEV [1964]).

Bacteria can sometimes be made visible in sliced or ground thin sections of undisturbed humus samples by staining. Staining methods can be of advantage also for the investigation of

Figure 28. Colorless aerial mycelium with strong autofluorescence (in the bright field transmitted light it is hardly visible). Dark aerial mycelium without fluorescence, emerging from a mycorrhiza mantle that surrounds an obliquely sectioned root. In addition, several bright plant residues fluoresce that likewise were hardly visible in bright field (the central cylinder of the root at the right fluoresces bluish green: lignin). Raw humus, F horizon (Black Forest, Germany). Ground thin section (15 μm), unstained, fluorescence illumination, natural size 600 μm.

colorless hyphae. MINDERMAN [1956] was able to recognize bacterial colonies in gelatin sections of a moder. According to ALEXANDER and JACKSON [1955], hyaline fungal hyphae, algal filaments, and also bacteria can be observed in ground soil thin sections if the soil is first stained and afterward carefully infiltrated with synthetic resin. The technique has been developed further by JONES and GRIFFITHS [1964]. With this technique they could investigate the distribution pattern of colonies of bacteria in soil aggregates. On the other hand, ground humus thin sections in which bacteria are made visible give an important insight into the questions of localization of microorganisms in the soil and into the micromorphology of humus formation by microorganisms. These questions are discussed by BARTHOLOMEW [1963].

Observations on these questions may, of course, be made with the help of *other techniques*, some of which have been used in soil microbiology for a long time. Among these are fluorescent staining of bacteria with Acridine orange in debris preparations of soil (STRUGGER [1949]) and the plate growth method (CHOLODNY [1930], ROSSI and GESUE [1930]). In the latter, work can likewise be done with fluorescent dyestuffs (LEHNER and NOWAK [1959]). For further details on these techniques, see textbooks on soil microbiology (*e.g.*, MÜLLER [1965]). In such preparations filmy and clusterlike colonies of bacteria may be distinguished (ROSSI [1936]). The colonization of dead plant residues by bacterial colonies may also be observed (GLATHE [1955]). TROLLDENIER [1965a, b] has been able to observe the colonization of living roots by bacterial colonies with the aid of fluorescent staining. Direct observations of an A_h horizon of a moder found that only 0.02% of the surface of the sand grains was covered by bacteria; by fluorescence microscopy the greatest part of the bacteria was found on organic particles (GRAY *et al.*, [1967]). The natural position of bacteria and fungi in soil was also shown by scanning microscopy (GRAY [1967]).

The occurrences of the shells of *diatoms* in ground thin sections from anmoor (Section V C) and of *thekamoebae* from moder and raw humus (Section V D 1) have already been mentioned (Section III A). *Green algae* and their residues have seldom been observed in ground thin sections (VAN DER DRIFT [1964]).

Residues of *pollen* were found in paraffin sections of peats in undisturbed samples (RADFORTH and EYDT [1958]). In other humus forms, pollen residues are also present, but in such small amounts that they can only be investigated microscopically after special enrichment methods (see textbooks and method books of pollen analysis, *e.g.*, FAEGRI and IVERSEN [1964]). Pollen analytical investigations on mineral soils were performed by WELTEN [1958]. Usually only the exine of pollens is preserved. It consists of sporopollenin (see Section III B 2 e). This substance, which is closely related to cutin and suberin, is degraded extremely slowly in acid soils (DIMBLEBY [1961]). VAN GIJZEL [1961] found a shift towards longer wavelengths in the fluorescence color of the pollen with increasing age. VAN GIJZEL [1961] interprets this shift by decomposition of some of the constituents of the sporopollenin. ERDTMAN [1971] observed hieroglyph-like corrosion structures in the exine, the outermost part of which seemed to be more resistant than the rest.

(d) Opaque Particles

In thicker ground sections aggregates of strongly colored fine substance particles sometime appear opaque. Such material might have been envisaged by HARTMANN [1965] when he speaks of "coal-like fine humus." Also a dense cover of opaque, granular material on poorly colored cell wall residues, as in rendzina moder, gives, at lower magnification, the impression of completely opaque particles (see Figure 47).

In addition, however, there are also massive, clearly demarcated individual particles that are black in incident light, and completely opaque in transmitted light, even in very thin ground sections of about 10 μm. Such particles may be found in the fine substance of nearly all

surface humus forms (BABEL [1964a]). They were also observed in water-logged mineral soils and in fossil peats (ALTEMÜLLER [1960], MOROZOWA [1963]; see also Part V C). They are often abundant enough to constitute an important fraction of the total material (up to some percent).

According to BABEL [1964b], some groups of opaque organic constituents, which are of very different origins, may be distinguished. Their identification is made possible partly by comparison with similar pieces having characteristic outlines or which are not completely opaque and thereby allow internal structures to be recognized. In other cases internal structures can be made visible by treatment with sodium hypochlorite (BABEL [1964c]).

Opaque formations from fungal *plectenchyma* frequently appear as fragments of sclerotial cortex as well as parts of mycorrhiza mantles and parts of perithecia (Figure 20). Other small fragments are derived from *charcoals* (Figure 17, cf. Section III B 2 d α). Blackened *cell parts* and *tissue parts* of higher plants occur preferentially in peats and wet moder formations. Sometimes, parts of them are somewhat transparent. Blackened wood pieces cannot always be distinguished with certainty from charcoals (see JONGERIUS and PONS [1962b]). Without doubt, in addition to carbonization, there are still other ways of rendering the residues of higher plants opaque. This is shown, *inter alia*, by fully opaque phlobaphenes in the cell contents of cork tissues, the cell walls of which are still colorless and birefringent. Also, opaque leaf residues with well-preserved mesophyll are found (Figure 14).

Chitin armour of animals can likewise be opaque, although this is very rare. More or less spherical, opaque formations of roughly 50 to 150 μm in diameter, which can occur in considerable amounts at the boundary between L and F layer, are enchytraeid and collembola droppings. They have apparently developed from very small-grained opaque impurities (grains of 1 to a few μm in diameter) which may be found in the L layer on the leaf surfaces (Figures 9, 6). These grains appear to be of microbial origin and are consumed together with the food by the animals named (ZACHARIAE [1963, 1964]). Easily confused with them are particles from technical fly ash, which can occur in densely populated and industrialized regions in the superficial horizons of soils. The differentiation of opaque organic constituents from opaque minerals is possible by means of sodium hypochlorite.

(e) Particles from the Solution Phase

In peats and related humus formations one finds morphologically homogeneous organic substances, which evidently represent pure formations from the solution phase. Morphologically similar constituents can occur in mineral humus horizons (see Section III D 2 b).

In holorganic terrestrial humus formations, in contrast, such constituents can be observed only seldom. The author has found red-brown, homogeneous organic substances forming 2 to 5 μm thick coatings on droppings (of diptera larvae probably) in spruce moder. In terrestrial humus formations, generally, dissolved organic substances are absorbed by the solid parts or they form more or less granular coatings on them, which are not distinguishable with certainty by micromorphological methods. Such coatings can contribute to the aggregation of individual particles. Spaces in rotting wood of stems and roots can be coated with films, which apparently are produced from soluble decomposition products of wood. This may be the case also in terrestrial humus forms. Such formations do not seem to have been accurately investigated.

Information on the formation of dissolved humus substances was presented in Section III B 2 a. It should be added that soluble substances are formed among others in the autolysis of bacteria (BARTHOLOMEW [1963]) and that KÜHNELT [1963] has detected water-soluble tannins among leaf residues of the upper F layer of a beech forest.

In peats there are precipitates of organic substances that have been formed from the

solution phase and that have often been described and illustrated (KUBIENA [1943a], JONGERIUS and PONS [1962a], GROSSE-BRAUCKMANN and PUFFE [1964]; see Figure 29). These formations are orange-yellow to brown. Because their interiors are completely structureless, their formation from the solution phase can be deduced. Sometimes they form only very thin layers. But in more strongly decomposed peats or in humus-enriched horizons of peats they are usually very dark to opaque. In these cases they have greater thickness and completely envelope the plant residues. Often the interstices between the plant residues can then be entirely filled. In ground thin sections, however, as well as in cremolan sections, such crusts show shrinkage cracks. KOWALINSKI [1964b], who has investigated humus enrichment horizons in peats, has found that in terms of humus chemistry these crusts must be designated as hymatomelanic acids.

3. *The Chemistry of the Fine Substance*

The chemical composition of the fine substance may be deduced from morphological analyses.

A considerable proportion of the fine substance is not appreciably altered chemically as compared with the plant residues. This is true of fresh droppings, in which the parts of plant residues, apart from disintegration and sometimes deformation, show no morphological changes. It is also true for the small tissue fragments, the histological origin of which can still be identified microscopically. In the morphologically completely destroyed material there is still present a considerable amount of unchanged cell wall substances, as is shown by the significant amount of cell wall fragments visible after removal of colored substances. By test reactions, cellulose can be detected (HANDLEY [1954]). In the H layer of a beech raw humus, the content of cell wall residues amounted to a quarter of the fine substance (BABEL [1965a]). The histochemical and histophysical investigations of these cell wall fragments showed that apart from cellulose they contain also cutin, and in rarer cases, lignin (see Table 4). In the A_h horizon the amount of cellulose in the fine substance decreases appreciably, and lignin is found only in traces (BABEL [1972b]). (This is in agreement with chemical results of KICKUTH *et al.* [1969], quoted in Part III B 2d).

The brightly colored parts of the fine substance are, for the most part, either unchanged or only slightly changed derivatives of those colored substances that may be found in the plant residues before disintegration. They are browning substances from the materials of the parenchyma cell contents, phlobaphenes and degradation products of lignified cell walls (see Section III B 2).

The increase in dark and dull-colored constituents with increasing depth in the profile of

Table 4. Results of the histochemical and histophysical analyses of the cell wall residues from the fine substance (< 200 μm) of a beech raw humus.

	Cutin-containing cell wall residues	Lignin-containing cell wall residues	Cellulose-containing cell wall residues
(Leaves from the litter)	(1)	(2–3)	(5)
Fermentation layer (F)	2	2	5
Humus substance layer (H)	3	1	4

Estimation scale of 1–5: 1 = little, 5 = very much. (From BABEL [1965a].)

surface humus formations, however, indicates oxidative changes. These, apparently, involve mainly the colored components, since cell wall substances may be detected as before.

It has been frequently recognized from soil biological studies that the chemical composition of soil animal droppings is not greatly different from the composition of the food which the animal consumed. Rapid changes occur, however, after the droppings have been deposited (KÜHNELT [1961], DUNGER [1964]). The microbial count and the activity of microorganisms are considerably higher in fresh droppings than in the parent material (VAN DER DRIFT and WITKAMP [1960], PONOMAREWA [1962], BIWER [1961]). The most important reason for the later changes in the droppings is accordingly to be found in a stimulated activity of the microflora.

A rise in the content of true humus substances (content of acetyl bromide soluble matter) is found only in aged droppings (FRANZ and LEITENBERGER [1948], discussed in KÜHNELT [1957] and DUNGER [1958]).

Mineralization processes during passage through the gut (BIWER [1961], PARLE [1963]) and morphological changes of individual parts from digestive activity by the animals (SCHUSTER [1956]) are only seldom determinable. The essential activity of animals for humus formation is not the chemical alteration but the creation of new physicochemical and microbiological conditions and new surfaces for autoxidation and microbiological reactions (*e.g.*, SCHUSTER [1956]).

The considerable proportion of dark-colored spores, plectenchyma, and especially hyphae of fungi that may be found in many surface humus formations signifies chemically the presence of chitin and fungal pigments and their degradation products in the fine substances.

Colorless fungal hyphae are decomposed much more quickly than colored ones, as MÜLLER [1887] concluded from his morphological investigations and as PINCK and ALLISON [1944] have detected in experiments (see also HURST and WAGNER [1969] and MEYER [1970]).

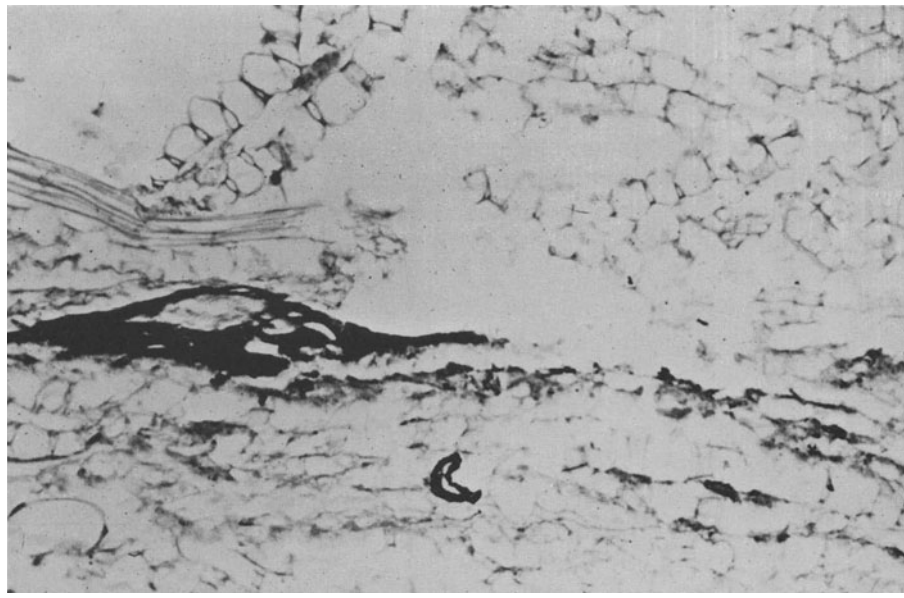

Figure 29. Sphagnum peat, slightly decomposed. Accumulation of strongly colored homogeneous substance from the solution phase (center left). Sliced section (Cremolan method, 10 μm), bright field, natural size 600 μm. (From a preparation by D. Puffe, Bremen.)

This difference, according to the last-named authors, is due to the content of humic substance-like pigments, which usually amounts to 20 to 30% in colored hyphae. The quantity of fungal pigments that is formed in a mycelium is dependent on various external conditions, *e.g.*, nutrition and microclimate (KÜSTER and HAIDER [1961], BUTIN [1961]). Chitinases are produced by many soil animals and soil fungi (DROZDOVA [1959], DEVIGNE and JEUNIAUX [1961]). They degrade chitin to acetylglucosamine and, from that, humic substances can be synthesized in melanoidin-like reactions. The relatively high amino sugar content, which was found by BREMNER [1955] in an acid soil, might be caused in particular by the high proportion of hyphae and hyphal residues that are usually found in such soils. Humus substance formation by microorganisms is treated extensively by SCHEFFER and ULRICH [1960]. They treat not only the formation of humus substance-like fungal pigments and fungal degradation products but also the formation of humus substances from aromatic compounds in the substrate by ecto-enzymes (see also HAIDER and MARTIN [1970], MARTIN and HAIDER [1971]). As is well known, the soil microorganisms are the most important producers of soil polysaccharides, which constitute often 10 to 30% of soil organic matter and which play an important role in soil aggregation (see MARTIN and HAIDER [1971]).

D. Organic Matter in the Mineral Soil

In the mineral humus horizon of mull as well as in deeper mineral soil horizons, the organic matter is more or less different from the organic matter in the holorganic humus horizons. These differences arise from fundamental differences in processes of formation. The morphology of the organic matter in mineral soil will accordingly be given special treatment here. This account can be composed briefly because reference can be made to the other sections, particularly to Parts IV and V. In addition, only few detailed investigations on this subject are available.

Sometimes organic constituents cannot be distinguished from mineral constituents purely by morphological means. There are, for example, opaque organic constituents and opaque minerals. There are further more or less homogeneous, reddish-brown formations, which may be phlobaphene-containing organic parts or iron oxide containing mineral parts. In such cases differentiation is possible by means of microchemical reactions which can be performed also on the ground thin sections such as the sodium hypochlorite and Prussian blue reaction (BABEL [1964c]).

1. *Blending of the Organic Matter into the Mineral Soil*

A considerable part of the organic matter is formed by roots and by microorganisms in the mineral soil itself. The amount of the root substance continually dying off is noted in Part III B1. The litter is mixed into the mineral soil by five processes:

1. Blending by animals.
2. Blending of solid particles by gravitation and rainwater.
3. Illuviation of dissolved substances by rainwater.
4. Processes of surface erosion on slopes.
5. Tillage.

These five processes are of very different importance in different humus forms. They are responsible for part of the most important characteristics of the humus forms.

Many animals in soil cause intermixing, but earthworms are considered to be the most important group. Depending on the species and the special conditions, their activities are extremely varied. Some earthworms (*e.g. Lumbricus terrestris*) draw plant litter into the soil consuming it later as food. On the other hand, droppings consisting mainly of mineral sub-

stances are often deposited in the F layer or even on the surface of the L layer (*e.g.*, ZAJONC [1967]). Some species make vertical burrows which are often lined with humus excrements. This results in blending of only small quantitative significance. Tipulidae larvae often deposit highly organic droppings in the upper soil horizon. (For details see the textbooks on soil biology by KÜHNELT [1961] and DUNGER [1964]; ZACHARIAE [1964].)

In forest soils earthworms usually consume material previously disintegrated by arthropods. They do not transport this material over large distances. Here the earthworms are of little significance in the intermixing of organic matter. Also by the simultaneous consumption of organic and mineral material they do not themselves bring about any mixing which would be of more importance to the macroscopic development of the soil profile (ZACHARIAE [1965]).

By the trampling and rummaging activities of game animals and the burrowing of mice and moles, in forests the litter can be intermingled in places to a considerable extent into the mineral soil (ZACHARIAE [1965]).

The mixing in of solid organic matter by gravitation and rainwater is a process by which great amounts are transported in all humus forms. In moder and raw humus organic fine substance from the H layer is washed into the small intergranular spaces of the upper 1 or 2 cm of the mineral soil (BAL [1970]). In mull, leaf and other small plant fragments fall into the larger interaggregate spaces which are continuously formed by the burrowing activity of earthworms in the upper 1 to 5 cm of mineral soils (ZACHARIAE [1966]). In Tirs and related soil formations (vertisols) shrinking fissures are of similar effect, whereby a self-mulching arises.

Movements of dissolved organic matter from the organic layers into the mineral soil take place in all humus forms. In mull they extend over distances of a few millimeters at most; in moder and raw humus over several decimeters (podzolization).

2. *Holorganic Constituents in the Mineral Soil*

(a) Plant Residues

Often root residues may be found. In the ground thin section it cannot be ascertained with certainty whether well-preserved roots were still living or dead. Frequently cast-off pieces of barks of old tree roots appear (Figure 15). Also, from the old grass roots the cortex sloughs off, leaving only the central stele (GADGIL [1965]).

The intermingled pieces of the litter can be still well preserved morphologically or they may show a progressive homogenization of the tissue structures.

Plant residues in pseudogleys and gleys are often infiltrated and encrusted to varying degrees by iron oxides (Figure 3). The infiltration extends in that case into the cell walls, as may be detected by the Prussian blue reaction (BABEL [1964c]). In semiterrestrial humus forms or those under water-logging conditions, often dark brown to opaque plant residues can be found (see Part V C).

The frequency of the plant residues changes greatly in the A_h horizon of a mull in the course of the year. It can be especially high in fresh earthworm droppings. Whether general differences in the frequency of the plant residues exist for different mull subforms cannot yet be definitely stated. In MÜCKENHAUSEN [1962], for the A_h horizon of pseudogleys, the humus form of which is, in general, a mull closely related to moder, a relatively large amount of plant residues is reported. In matted mull (BARRATT [1964]) under grassland large amounts of dead roots occur.

(b) Organic Fine Substance

In the upper centimeters of the mineral soil of moder and raw humus organic substances

occur prevailingly as intrinsic fine substance particles. Morphologically it resembles very much the fine substance of the H horizon. But very small grains (about 1/2 μm), which cover organic fine substance particles, are translucent here, whereas in the H horizon they are opaque (BABEL [1972b]). In the lower parts of the A_h horizon the whole material is lightened, probably by decomposition or displacement of organic substance (BAL [1970]).

Just as with plant residues, holorganic fine substance particles in the A_h horizon of mull are, as a rule, rare. They may be detected, rather than in thin sections, by fractionating by specific gravity. MCKEAGUE [1971], by those methods, found small cell and tissue residues in the silt fractions of Canadian chernozems (compare also BOTTNER [1970]).

Readily identifiable particles that are found relatively frequently are the reddish-brown cork and cortical cells of roots, described in Section III C 2 a. Dark hyphae of fungi occur especially at the upper boundary of the B_h horizon of posdols (ALTEMÜLLER [1962]). In acid- and water-influenced humus formations, there are remarkable amounts of colorless cell wall residues, which often become visible only in the fluorescence microscope by their blue or also yellowish primary fluorescence (Figure 30; BABEL [1972a] see also ALTEMÜLLER [1960]). In low amounts such particles also occur in other humus formations.

Opaque or dark-brown transparent plant fragments of the size of one or a few cells were observed likewise in water-influenced mineral soils (cf. Section III C 2 d; Figures 31, 49).

Very small dark particles, less than 1 μm in size, were observed in the agriculturally cultivated humus horizon (A_p) of a mull-pararendzina (ALTEMÜLLER [1960]) and in the humus cutans of para-brown earths (ALTEMÜLLER [1956]). In the widespread forms of mull, particles of this kind, however, do not occur. They were found, however, in several soil types by PARFENOVA and YARILOVA [1967]; 2 to 3 μ brownish-black organic particles in southern chernozem soils seemed to be especially characteristic.

Around the mineral grains in the B_h horizons of podsols, coatings of organic matter with

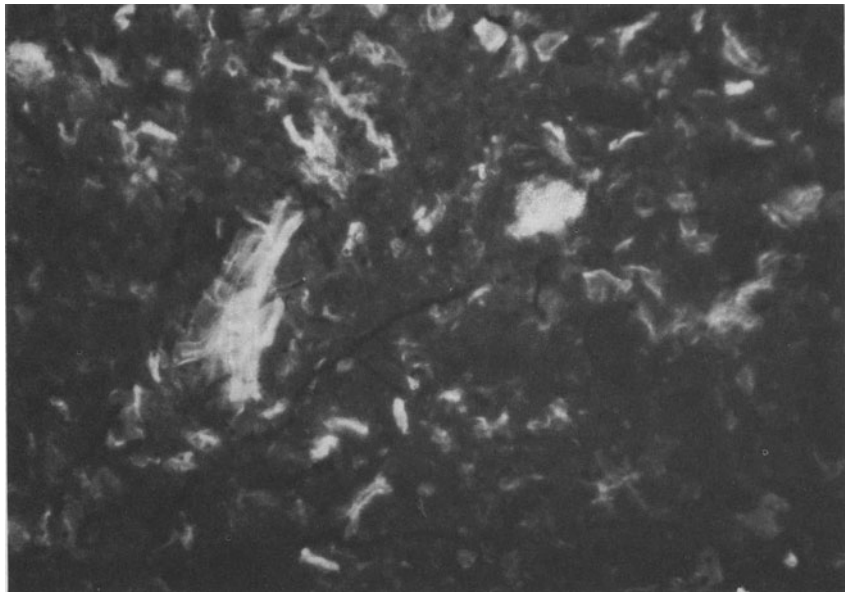

Figure 30. Numerous fluorescing, strongly crushed cell wall residues in the back water horizon of a pseudogley (dense silty loam; carbon content 1%). The cell wall residues are remains of fine roots. They are not visible in the bright field. Very dark: fungal hyphae (central uplands of Germany). Ground thin section (30 μm), primary fluorescence, natural size 400 μm.

clear yellow to brown colors are formed from the solution phase (covered fabric, see Part IV B3 and Figure 45).

3. *Organic Matter as Pigment of the Mineral Fine Substance*

In mull and related humus formations a substantial proportion of the organic matter is present as pigment of the mineral fine substance, which shows no holorganic particles, even with the strongest microscopic magnification.

Electron microscope pictures suggest that in this material a morphological separation of organic and mineral particles exists only at 0.01μm or below. (DUDAS and PAWLUK [1969, 70a] obtained particles with irregular and indistinct contours before and sharp contours after peroxide treatment.) For discussion of the arrangement of sesquihydroxides, humus, and clay minerals in the submicroscopic range, see HESS [1965]. From clay mineralogical investigations the localization of organic matter in the interlayers of montmorillonite can be concluded (GEBHARDT [1971]).

In mull practically the whole of the organic matter has been transported in the solution

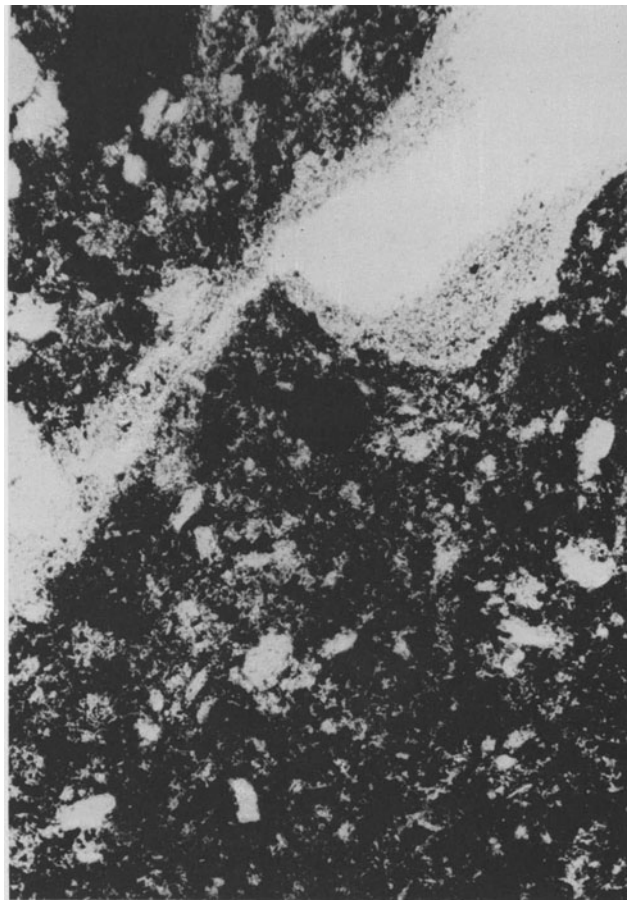

Figure 31. Fossil wet humus formation with numerous small opaque organic constituents in the strongly colored mineral fine substance (these cannot be distinguished in the photograph). The walls of a channel (top left) with humus-poorer, hence brighter cutan. Colluvial clay (central uplands of Germany). Ground thin section (20 μm), bright field, natural size 600 μm.

phase, although only over the smallest distances, then to be precipitated at the surfaces of the clay minerals and the oxide hydrates. There, catalytic transformations of the organic compounds and the formation of clay-humus complex occur (see SCHEFFER and ULRICH [1960].)

The main object of humus microscopic investigation of mull, therefore, is the fabric analysis (see Part IV).

From the colors of the mineral fabric components, inhomogeneities in the distribution of organic matter can be recognized (Figures 31, 49; see also Part IV B3). Thus, cutans of channels can differ morphologically from the interior fabric by a darker color. According to ALTEMÜLLER [1956], the degree of their orientation birefringence decreases with increasing depth of color and hence increasing humus content.

IV. Fabrics in Humus Soil Horizons

The organic constituents dealt with in the preceding section, alone or together with mineral constituents, build up the fabric of the humus soil horizons.

The term fabric is used here, according to ALTEMÜLLER [1962], to be the arrangement of the constituents. According to KUBIENA [1935, 1938], elementary fabric (grouping of the single parts to each other) and aggregate fabric (formation and arrangement of the aggregates) may be distinguished. A comprehensive treatment of the terms "texture," "structure," and "fabric," as well as the bases of the fabric analysis, are given by BREWER [1964].

Here, only a brief treatment of those soil fabrics greatly affected by organic substances and organisms will be given. The most important phenomena of fabric formation and of typical fabric forms will be treated according to present knowledge in micromorphology. Too little is known about fabric systems to give a complete account of them (see Part IV C).

A detailed and systematic treatment of soil fabric is given by BREWER [1964]; but he gives little attention to organic matter and organisms. The same holds true for the treatment of soil fabric by ALTEMÜLLER [1966].

The fabric is determined by ratio, size, shape, and arrangement of the solid constituents and the pores. Fabric analysis of the horizons of the humus profile can provide information of biology and dynamics of humus formations.

The changing of fabrics from above downward in moder profiles has been investigated by macro- to micromorphological techniques and by estimating the changing amounts of some fabric features in the subsequent horizons (BABEL [1972b]). Micromorphometric measurements of those features have been carried out by several authors. KUBIENA, BECKMANN, and GEYGER [1962], by means of structure photograms, compared the fabrics of a brown loam, influenced by small animals, with the unaffected parts. JONGERIUS [1963], on the basis of such measurements, compared different humus forms, and BAL [1970] compared different subhorizons of a profile. GEYGER [1967] made comparative micromorphometric investigations on the biology and dynamics of alpine råmark.

A. Processes of Fabric Formation and Stabilization

The fabric of the organic soil horizons is built up and stabilized by biological and nonbiological forces. These forces often work against each other. They produce different types of fabric. Those formed biologically are often the more favorable from an ecological point of view (BENECKE and BABEL [1969]).

1. *Nonbiological Processes*

The nonbiological processes of fabric formation arise from swelling, shrinking, frost, and

surface tension of water. These actions can be modified considerably by organic substances (Figures 46, 41, 42).

Experiments of JABLONSKI and RADOMSKA [1965] showed the formation of pores around plant residues that occur in mineral soils. This was explained by the differences of swelling and shrinking of organic and mineral substances. Soil aggregates are stabilized by organic substance (as pigment) against breakdown by nonbiological forces. Fissures nevertheless arising from shrinking will have rough walls (see soil fabric classification by BECKMANN and GEYGER [1967]).

By action of water meniscuses leaves are stratified very densely in the lower L layer (L_v according to BABEL [1971a]; Figure 33). Over the very close interstices, which are formed in this way, other binding agents become effective (very small amounts of fine substance, slimes of microorganisms, precipitations of leaf leachates (BABEL [1972b]) which bind the leaves even after drying. Action of surface tension plays a role also in the compaction of the dropping fabric of enchytraeidae. During drying, the loosely lying droppings are drawn together by the surface tension of the water (BABEL [1968, 69]; see Part IV B 3).

By displacement of humic clay material humus containing coatings are formed on pore walls in the lower soil horizons. Displacement of dissolved organic matter gives rise to formation of the covered fabric in podzols.

2. *Fabric Formation by Roots and Microorganisms*

Roots bind soil aggregates, especially where they are strongly branched and have developed root hairs or mycorrhiza. The root epidermis often forms a slimy "mucigel layer." This creates a very close union between roots and substrate (electron microscopic investigations by JENNY amd GROSSENBACHER [1963]). APINIS [1969], in a comprehensive review of literature, points out that there is also indirect influence of roots on soil aggregation, as roots promote the development of rhizosphere organisms and these promote a better aggregation.

Biopores develop in places where roots decay (SLAGER [1964], GADGIL [1965]). These

Figure 32. Dark aerial mycelium in the L_vF_r horizon of a dry raw humus (produced under a *Pinus nigra* plantation on a former mull). Needle residues (transverse) and several roots (black-appearing structures, some transverse, some oblique); these parts are combined by the mycelium in a loose network (central uplands of Germany). Ground thin section (35 μm), bright field, natural size 1.5 mm.

are frequented by animals (*e.g.*, enchytraeidae), which loosen the surrounding mineral material.

On the other hand, growing roots cause a compaction of soil in their close environment (micromorphometric investigations of BLEVINS *et al.* [1970] on tree roots with a diameter of 4 to 7 mm).

Microbial filaments (bacterial colonies, actinomycete and fungal hyphae, algal filaments) contribute to living obstructions (SEKERA and BRUNNER [1943]). Numerous fungal hyphae may be observed microscopically, and often may be seen with the naked eye. Often they permeate both the plant residues of the lower L layer (L_v) and the upper F layer (F_r, according to BABEL [1971a]), as observed for instance by MEYER [1962] (Figure 32).

In A_h horizons fungal hyphae occur to combine sand grains (BARRATT [1962]) or primary aggregates (enchytraeidae droppings, BENECKE and BABEL [1969]). Rhizomorphae may act in the same way as hyphae. As in the case of roots, often a slime layer intensifies the binding action of the hyphae (ASPIRAS *et al.* [1971]); it consists of mycofibrillae (LIESE and SCHMID [1962]). With the electron microscope BEUTELSPACHER [1955] found microbial linear colloids combining mineral particles.

Pores may be formed by fermentation activities of microorganisms as was found by JEANSON [1964] in experiments in dense soil fabrics. (For further details on the influence of microorganisms on soil fabric, see textbooks of soil microbiology.)

3. *Fabric Formation by Animals; Droppings*

Animals living in soil exert a profound influence on the soil fabric by many of their activities. By their metabolic activities they change the organic constituents (see Part III C 1 a); by their blending activity they displace soil particles (see Part III D 1). By their movements in the soil they form channels. In biologically active soils the movements of the animals—including those which pass only a short period of life in the soil—can produce a strong loosening effect and the formation of roll aggregates (ZACHARIAE [1962]). The most important contribution, however, to fabric formation given by the soil animals are their excrements. These are the prevailing primary aggregates of many humus horizons.

The excrements of soil animals (at least if they are noticeable through their characteristic forms) are usually called droppings ("Losungen") in the German micromorphological literature; in the English literature, fecal pellets. They have been recognized since the studies of KUBIENA [1943a, b] as characteristic features for the biology of natural humus formations. Nearly all micromorphological publications on natural humus formations contain observations on droppings. Among them, however, detailed studies of these objects are rare.

Often droppings are found directly at the feeding places, especially in feeding cavities within plant residues (wood fragments, roots, needles, stem bases, and in dense packets of leaves). Those examples are usually produced by oribatid mites (Figure 33, further illustrations, *e.g.*, in PUFFE and GROSSE-BRAUCKMANN [1963]). In other cases droppings can accumulate to such an extent that they form whole horizons (*e.g.*, the H layer in pitch moder; see Part V D 3). Then the term "dropping fabric" is used (Part IV B; Figure 40).

The nature of the active animal groups may often be determined from the size, shape, internal structure, and arrangement of the droppings as well as from the food traces in the substrate. An unequivocal determination, however, is frequently possible only if the fauna of the humus formation under investigation was identified at least approximately. Taxonomically very different animal groups often produce very similar droppings, *e.g.*, enchytraeids and collemboles (ZACHARIAE [1964]) or diplopods, Tipulidae larvae, and the earthworm Dendrobaena (ZACHARIAE [1967]). The appearance of the droppings is also greatly dependent on the composition of the food. Finally, droppings are often partially or wholly destroyed very soon after

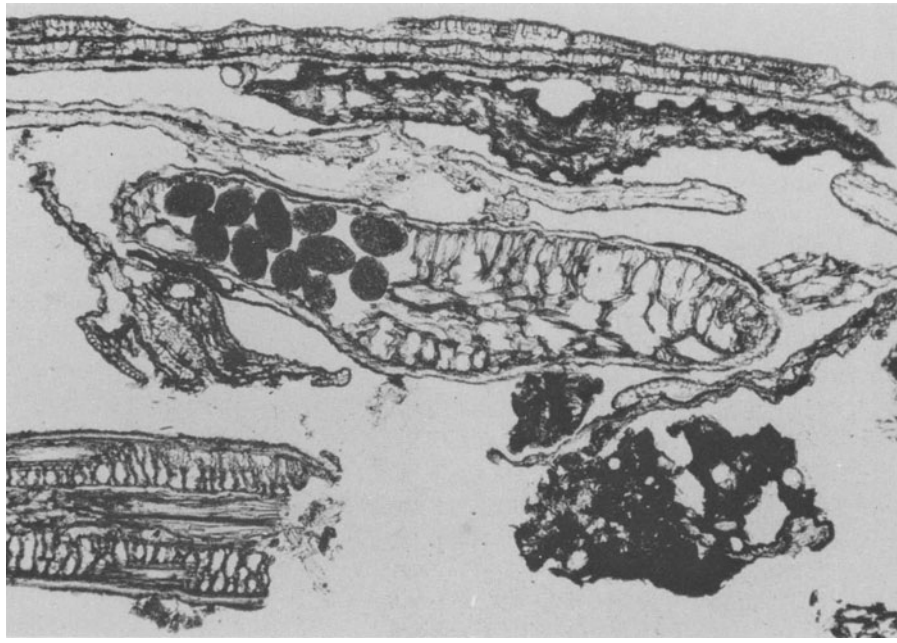

Figure 33. Mite droppings in a feeding cavity in the place of the assimilation parenchyma of an *Abies* needle (transverse; see also Fig. 34). To the right, the assimilation parenchyma is still well preserved, only browned. The droppings are of the same color (they seem to be darker because of the compaction of the material). The epidermis is intact throughout. Above that, a much shrunken *Abies* needle (likewise, transverse). Between these two the compressed residues of a needle, of which practically only the epidermis remains (thin, bright, leading out of the picture at the left; probably decomposition by fungi). At the top a densely compacted layer of three beech leaves, the uppermost collapsed in parts. Wet moder, F_r (Black Forest, Germany). Ground thin section (25 μm), bright field, natural size 1.5 mm.

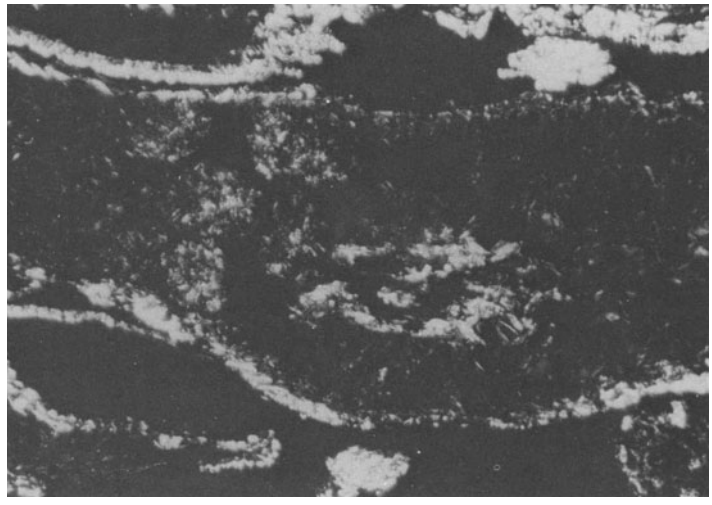

Figure 34. Detail of Figure 33, crossed polarizers. Also in the droppings the cellulose is still preserved (birefringence).

deposition. More precise investigations of dropping forms must therefore take into account the living and nutritional condition of the animals in their natural habitat; as an example of such a procedure, see the detailed work by ZACHARIAE [1965] already quoted.

In the following rough description of the dropping forms of the most important groups of soil animals (KÜHNELT [1958, 1961], DUNGER [1963], ZACHARIAE [1965]), the limitations mentioned should be taken into consideration.

The droppings of litter-consuming *diplopods* are among the most striking of droppings that one can come across in ground thin sections (Figures 37, 52). They are 0.5 to 4 mm in size. Sometimes they are built up by fairly large well-preserved plant fragments. Often they also contain mineral grains. They show a rather loose internal fabric. The contours of droppings are different in the individual subgroups of diplopods: The droppings of the large julids and glomerids are egg-shaped, those of the small julids more cylindrical, those of the polydesmids flattened. The droppings of the *isopods* are often very similar to those of the diplopods in respect to size and good preservation of the plant fragments. When well formed they are often flattened and sometimes show a longitudinal cleft.

Diptera larvae produce as many different types of droppings as there are different systematic groups on the one hand and different food on the other.

Detailed studies of gut contents of several groups of diptera larvae have been performed by HEALEY and RUSSEL-SMITH [1970]. They found different proportions of food residues (leaf fragments, fungal hyphae, very finely divided humus material, mineral material), not only in relation to different animal groups but also to the position in the humus profile and to the humus form.

Sometimes the droppings consist of very well-preserved tissue residues and therefore resemble diplopod droppings (Figure 38). When the larvae feed on more strongly predecomposed plant residues, the droppings contain much less recognizable tissue fragments. Mineral particles frequently occur in them. The droppings of Tipulidae larvae are egg-shaped. Bibionidae larvae produce cylindrical droppings, which sometimes fall apart easily. Investigations by SZABO *et al.* (1967) revealed that they contained leaf residues, some algal filaments and structureless organic substances and mineral particles. They were about 0.2 to 0.3 mm in diameter and up to 1 mm long. The droppings of lycoriidae larvae form, when wet, a pulp containing still easily recognizable cell residues. Under some circumstances it resembles fine substance formed out of enchytraeid droppings poor in mineral substance, which have subsequently fallen apart and welded together.

In ground thin sections the egg-shaped droppings of *oribatid* mites are recognizable with certainty (Figures 33 and 36). They are between 30 and 150 μm long and appear much denser than diplopod droppings—as the plant fragments contained, although still recognizable as such, are more disintegrated. They do not contain mineral particles. These droppings, as mentioned, often occur within feeding cavities according to the microhabitats of the animals (ANDERSON [1970]). There they form groups, a characteristic of which is that often a number of equally large droppings lie together, whereas neighboring parts consist of droppings of another size. These differences are probably caused by the progressive growth of the participating animals (ZACHARIAE [1965]).

Droppings of *collembola* are dark to black spheres, granular aggregates, or blotches of about 50 to 180 μm in size (Figure 35). They occur particularly in the lower L layer. Usually in ground thin sections they are opaque and no cell residues can be recognized. The food was slime films and microorganisms that had developed on the surface of plant residues. Partly, however, the droppings also show fungal hyphae or spores, or small birefringent cell fragments when the food was fungi or the mesophyll of leaves respectively (ZACHARIAE [1964]).

The droppings of *enchytraeids*, which live in the lower L layer on the same food as col-

lembola, are very similar. A fairly reliable distinguishing feature from collembola droppings is that the enchytraeid droppings are often arranged in two parallel rows, thus forming channels among the leaves for the accomodation of the animals (ZACHARIAE [1964,1965]). In the F and H horizons, where the enchytraeids are active as secondary decomposers, they produce granular droppings (Figure 39). Here very small cell wall residues are easily recognizable, at least by fluorescence microscopy. In mineral soils the droppings are rich in mineral substance (mineral grains up to 60 μm in size) (Figure 44). The droppings are about 40 to 100 μm in size with most of them being 60 μm.

Granular to egg-shaped aggregates of about 60 μm in humus soil horizons probably will be in most cases enchytraeid droppings (observations of the author in central Europe). In the H horizon, as well as in the A_h horizon, great parts of the fabric often are built up of enchytraeid droppings (Part IV B) (BABEL [1968, 69]). In the mineral soil the enchytraeids often follow the channels of dead fine roots and leave their droppings there. They eat themselves into earthworm droppings, creating channels which they then fill with their own droppings (ZACHARIAE [1964, 1965]).

Among the *lumbricidae*, *Dendrobaena* species in the L layer form droppings which are similar to but larger than the dark enchytraeid droppings and, like them, are often arranged in channels. But if *Dendrobaena* in the F layer consume the material disintegrated by arthropods, their droppings are egg-shaped to cylindrical. They can be very similar to the droppings of Tipulidae larvae (ZACHARIAE [1967]). Leaf residues in the L layer can be glued together by the droppings (or "castings") of the great *Allolobophora* and *Lumbricus* species.

The earthworm droppings deposited in mineral soil horizons are usually strongly compressed. Skeleton grains and fine substance often are arranged in concentric lobes that are parallel to the former surface of the droppings (ZACHARIAE [1967]). Between the droppings, small wedge-shaped pores generally remain free. Where the droppings are deposited in the F or L layers or on the soil surface, they form the well-known knobbly racemose forms (see also Part V D 5). In the upper part of the A_h horizon earthworm droppings and their residues are often combined to form spongy fabric (Part IV B 3; Figure 2). Lumbricidae droppings can contain plant fragments, one to several millimeters in size; *e.g.*, well-preserved pieces of leaves. Still larger plant residues can be enclosed between the dropping material by the deposition of droppings in F and L layers. In earthworm droppings the proportion of plant fragments and of mineral material varies greatly.

Other important fabric features produced by earthworms are the channels, which are built in the mineral soil by the large species. There are detailed treatments of them in the textbooks of soil zoology. The walls of the channels often are covered by humus clay material, which originates from excrements (HENSEN [1882]).

The increase of pore volume of soils by earthworms is caused by deposition of droppings on the surface, by the permanent burrowing activity in the upper few centimeters of the mineral soil, and by the channels that go down to the C horizon. Deposition of droppings in the mineral soil, however, causes local soil compactions. JEANSON [1964, 1970, 1971] in laboratory experiments has investigated the fabric formation by earthworms, especially the earthworm channels in thin sections and by scanning microscopy.

The position and arrangement of droppings with respect to other droppings and to other fabric components can contribute to the indentification of animal groups. Moreover, the location of droppings near tissues can give a hint to the food consumed by the animal (Figure 33). The morphological comparison of the dropping material with the preserved tissues gives hints to chemical alterations (Part III C 1a).

Micromorphological investigations of droppings often have ecological objectives, concerning autecology of certain groups of soil animals as well as ecology of humus formation and

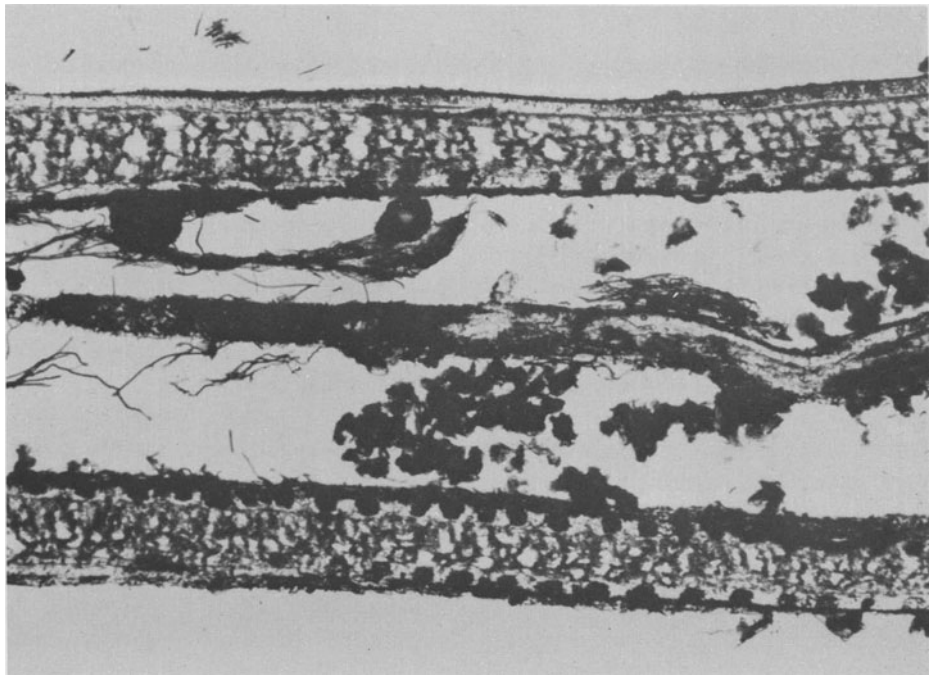

Figure 35. Collembola or enchytraeid droppings, consisting to a large extent of fungal material, which the animals have consumed from the surface of the (longitudinal) *Pinus mugo* needles. Left, dark aerial mycelium. Tangel, L_v horizon (Alps). Ground thin section (50 μm), bright field, natural size 1.5 mm.

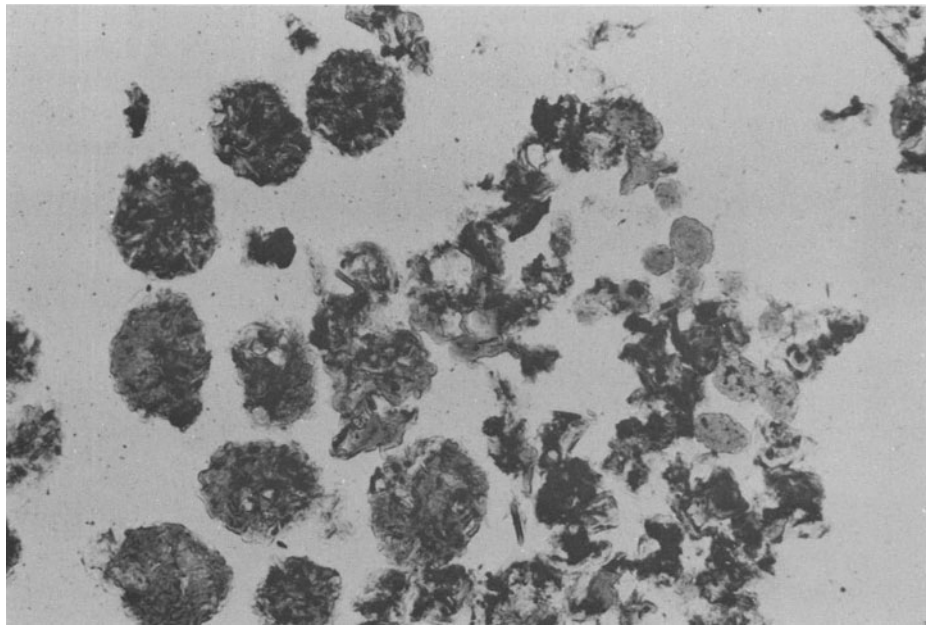

Figure 36. Mite droppings of different sizes and colors corresponding to different size of animals and different food. (Compare also Figure 33). *Picea* moder, F_r. (Northwest Germany). Ground thin section (12 μm), bright field, natural size 450 μm.

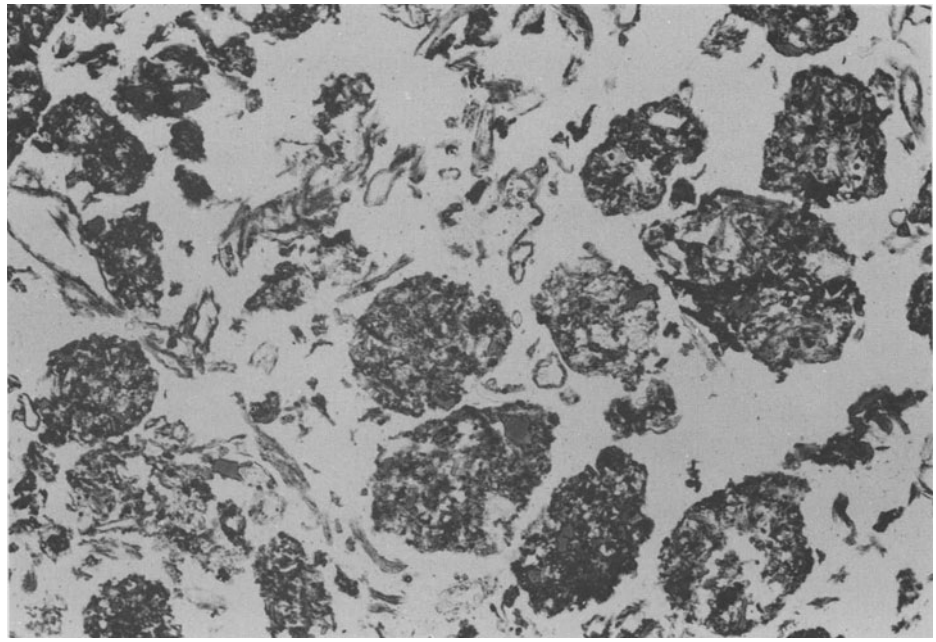

Figure 37. Droppings of isopods or diplopods (compare Figure 52). The stalked or ring-shaped parts between the droppings are for the most part fine roots of herbaceous plants. A moderate proportion of small mineral grains in the droppings is not visible in the bright field. H_r, moder to mull-like moder (central uplands of Germany). Ground thin section (15 μm), bright field, natural size 1.5 mm.

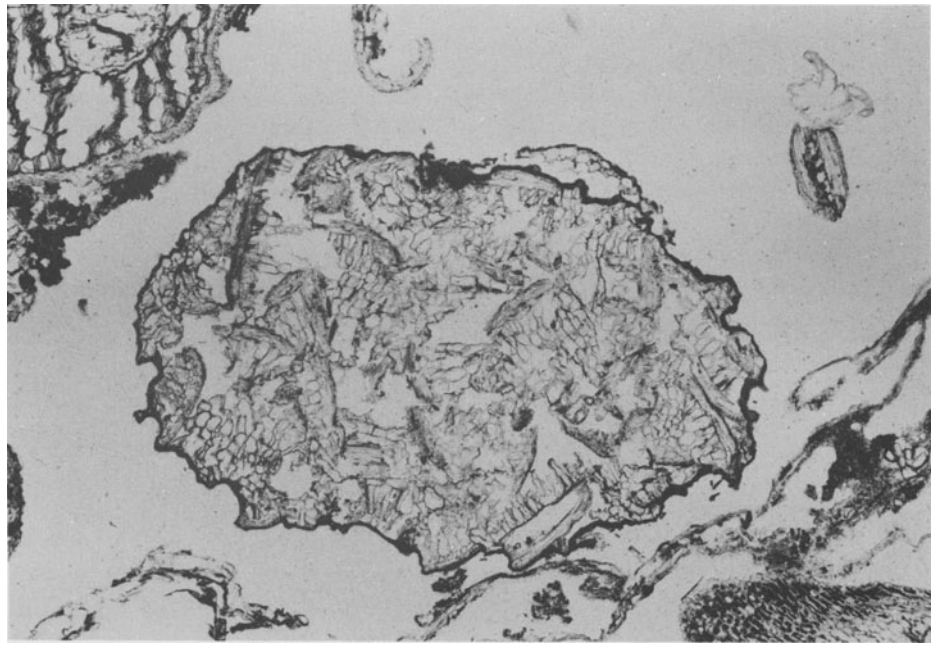

Figure 38. Dropping of a diptera larva, containing scarcely changed tissue fragments of spruce needles, encased by a peritrophic membrane. Spruce moder, F_r (central uplands of Germany). Ground thin section (12 μm), bright field, natural size 2 mm.

ecology of the whole site. Some examples of evaluation of dropping investigations for ecological aims are given by ZACHARIAE [1967].

Droppings of primary consumers usually are consumed (eaten) by secondary decomposers after a short time and thus are changed to other dropping forms. Mechanical influences cause formation of clusters out of the droppings or cause their breakdown (*e.g.*, Figure 43). Breakdown is accelerated by processes of decomposition and dissolution (BAL [1970]). Also, fungal hyphae can destroy the droppings by growing into them. JONGERIUS and SCHELLING [1960] observed that the droppings fall apart more quickly in acid humus formations than in eutrophic ones. RIGHI [1969] observed that the droppings fall apart readily in wet humus formations on podzols but are preserved for a longer time in dry ones.

Great amounts of droppings do not necessarily indicate great animal activity. Even under very favorable conditions, when further transforming organisms are absent, droppings can accumulate appreciably in only slightly altered form, as ZACHARIAE [1965] has shown for droppings of enchytraeids and arthropods. This may also be the cause of the great amounts of droppings in alpine råmark (transitions from raw soil humus to moder and mull-like moder), which has been found by GEYGER [1967].

After the breakdown of droppings, a new formation of aggregates from the fine substance may often be found, but a compaction of the whole material may also occur (Figure 41; PUFFE [1965]).

B. Fabric Types in Humus Soil Horizons

Here only the well-known typical fabric forms will be described. The present state of knowledge does not allow us to give a comprehensive picture.

1. *Fabrics with Plant Residues Prevailing*

Laminated fabric of plant residues is characterized especially by a large proportion of more or less horizontally placed plant residues, particularly leaves (Figures 33 and 1). These are still preserved in rather large, macroscopically visible pieces. In some parts they can be compacted very closely, so that neither pores nor binding substances can be seen between them with a microscope. In other parts hyphae or organic fine substance are found between the plant residues. The fine substance regularly lies on the surfaces of the plant residues and joins them together in the form of bridges or larger masses. This fabric comes about by action of water films between the leaves in the L_v horizon, as well as by deposition of animal droppings which feed on microorganisms on the leaf surfaces. It offers suitable environmental conditions to the litter-disintegrating animals and is destroyed by them gradually (BABEL [1972b]).

2. *Fabrics of Organic Fine Substance*

Dropping fabric consists of granular or egg-shaped droppings that are nearly equal in size and shape (Figure 40). Most frequently found sizes are about 60 μ. There are types with different degrees of compaction. In most cases the droppings are more or less welded and in places their contours are not well preserved. Figure 40 is a typical example. Figure 39 shows a highly porous example, where the granular aggregates of fine substance can scarcely be identified as droppings. In dense forms of this fabric, formation of fissures is observed. This fabric is frequent in the H horizon of moder. It is especially well developed in pitch moder. (It also occurs in mineral soils; see Part IV B 3.) Enchytraeids are especially important in building up this fabric. They act as secondary consumers of material, which has been formed in the F layer by litter-disintegrating animals.

In other cases organic fine substance can form a *dense fabric* with very small pores which originate by the contours of the single particles (single packing voids of BREWER [1964]). Besides, the fabric is divided by shrinking fissures (Figure 41). This fabric occurs above all in the H layer of wet moder forms; it develops by breakdown of the droppings.

3. *Fabrics in Humus Mineral Soil Horizons*

The differentiation of fabrics in mineral soils is greater than in the humus layers because of the addition of mineral components and because of the activity of larger soil animals, especially earthworms.

There are manifold forms of pores and aggregates. Channels (BREWER [1964]) are formed primarily by activity of organisms (roots or animals). If refilled, they are called pedotubules by BREWER. The material of the pedotubules often is darker (richer in organic matter). Sometimes it appears striated (striotubules: earthworm excrements), sometimes it is aggregated in the form of droppings or in similar forms (aggrotubules: excrements of earthworms and smaller animals). (See investigations of GHITULESCU and STOOPS [1970].) The walls of earthworm channels are covered by humus material deposited by the earthworms (see also Part IV A 3). Cutans of dark, peptized clay rich in humus are formed by deposition by seepage water (organo-argillan of BREWER). Thin humus clay cutans were found in chernozem-like soils and (more intensely developed) in para-brown earth (ALTEMÜLLER [1956], KUBIENA [1966], PARFENOVA and YARILOVA [1967]). Humus wall deposits are also described by KARPATSCHEWSKI [1960] and JONGERIUS and PONS [1962a] in muck mull.

The *agglomeratic fabric* (KUBIENA [1938], by BREWER [1964] called agglomeroplasmic fabric because of confusion with the definition in geology) is composed of loose-lying, more or less uncovered mineral grains between which loose-lying organic fine substance is deposited in small flaky to granular aggregates (Figure 43). Aggregates of a higher level are not formed out of these components. This fabric occurs when in the mineral humus horizon of raw humus and moder the mineral component is a sand. Besides, it occurs on the upper border of the B_h horizon of podzols. RIGHI [1969] supposes that it is formed there by transformation of the covered fabric by animals. Normally the agglomeratic fabric develops by illuviation of solid organic particles from the H horizon into the mineral soil. In this process dropping forms are more or less preserved, or they may be newly formed after depositing.

The *spongy fabric* (KUBIENA [1938]; for microphotos see also KUBIENA [1970]) is characterized by manifold racemous forms of aggregates that are connected to each other by irregular bridge formations. From this a manifold pore system results (Figure 2). Often bulbous and indented residues of coprogenous contours are found. By mixing aggregates of different color (by different humus and iron content) a mosaic-like pattern is often formed (ZACHARIAE [1965]). This is found mostly in dense forms (pore structure of BECKMANN and GEYGER [1967], see Part IV C). Sand grains, if they are present, do not occur free, but are incorporated into the aggregates. Plant residues are not frequent. In very loose forms (transitions to crumb structure (BECKMANN and GEYGER [1967], Part IV C) they lie in places free in the pores, or they are incorporated in the mineral aggregates. Particles of organic fine substance seldom occur. The main part of the organic substance occurs as pigment of the mineral fine substance (Part III D 3). The fabric is formed prevailingly by the burrowing activity and depositing of droppings of great earthworm species (in central Europe, above all, *Lumbricus terrestris* and *Allolobophora terrestris*). Sometimes the small droppings of enchytraeids are found in places especially rich in organic matter (ZACHARIAE [1965]).

A *dropping fabric* from enchytraeids in loess was described by BABEL [1968] (Figure 44). It is built up by enchytraeid droppings about 60 μ in size, which are the primary aggregates. These can lie very loosely, they can be welded weakly, or they can lie so compactly that the

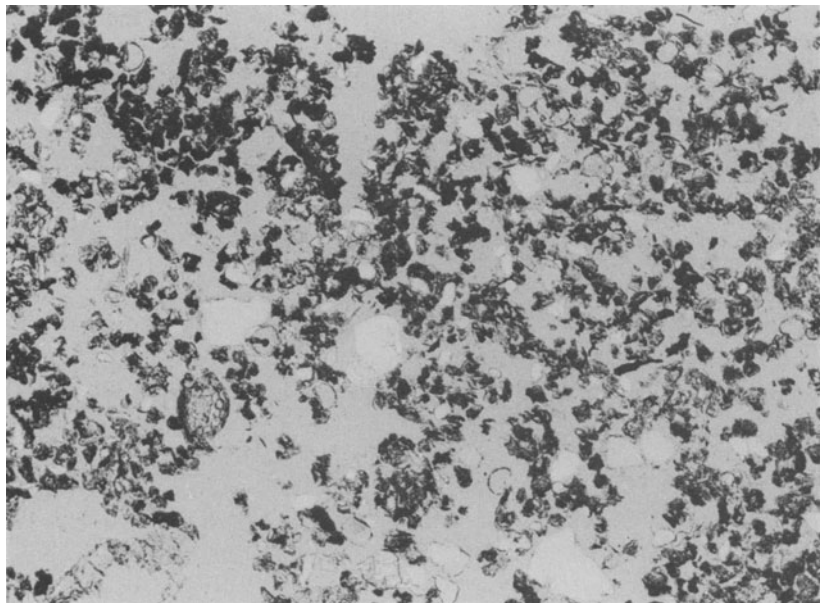

Figure 39. Loose dropping fabric (related to agglomeratic fabric; see also Figure 23). The small granular aggregates are enchytraeid droppings. Moderate proportion of quartz grains. *Picea* moder, H/A_{hh}. (Northwest Germany). Ground thin section (20 μm), half-crossed polarizers, natural size 1.5 mm.

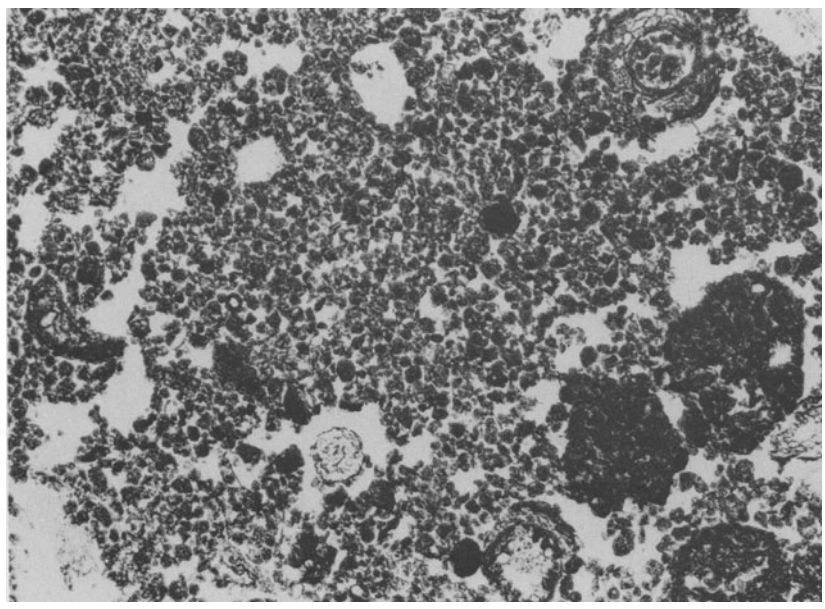

Figure 40. Dropping fabric. Nearly the whole material consists of moderate to well-preserved small droppings (of enchytraeids?) bottom right, two large droppings. Three transversely occurring roots. Pitch moder, H_f (Alps). Ground thin sections (25 μm), bright field, natural size 1.5 mm.

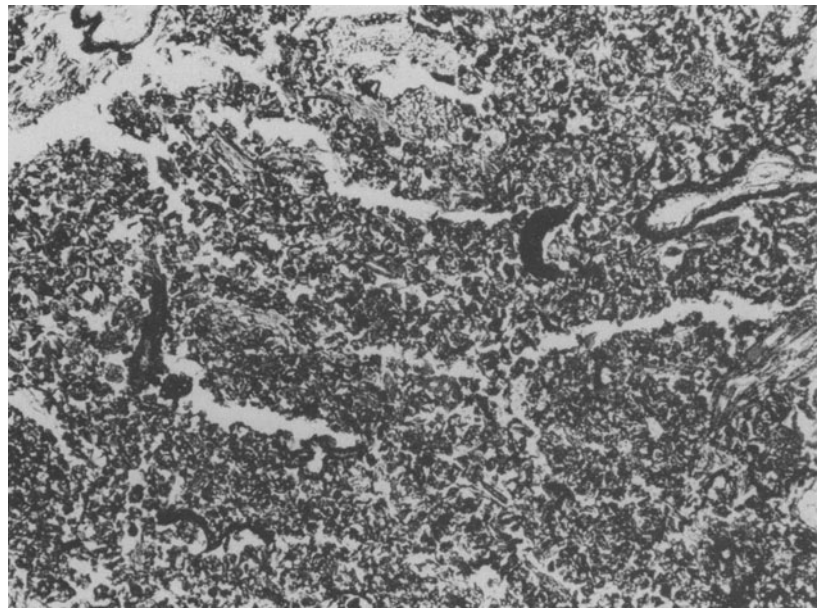

Figure 41. Dense fine substance fabric, with horizontal cracks (see also Figure 25). Of plant residues, only root residues of different sizes may be recognized. The fine substance has developed from droppings, which have fallen apart; the size of the particles corresponds to the bite size of the animals (compare Figure 40). Pitch moder, H_f (Alps). Ground thin section (25 μm), bright field, natural size 1.5 mm.

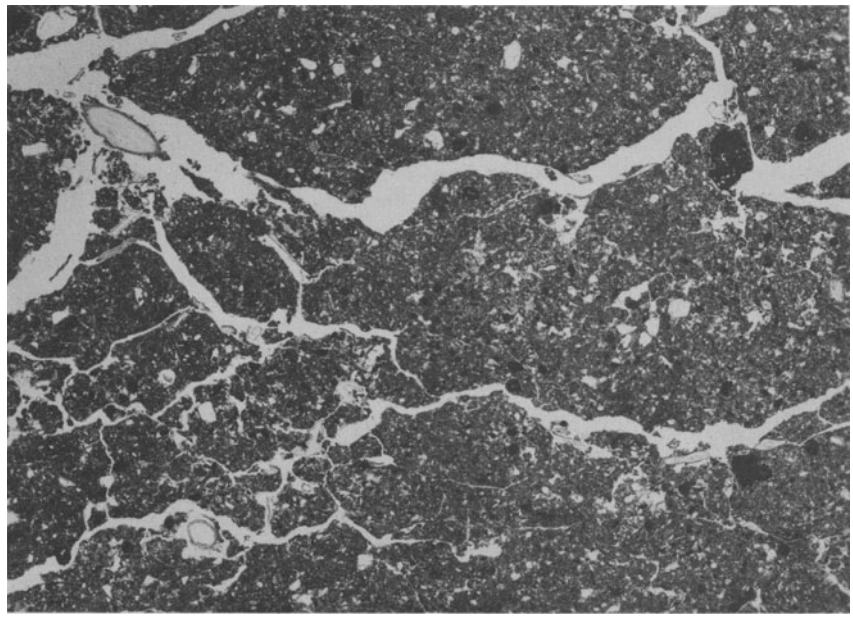

Figure 42. Mull, dense fabric with numerous cracks, which are often used by roots. *Terra fusca* A_h (4 cm) (Austrian limestone alps.) Ground thin section (25 μm), bright field, natural size 5.5 mm.

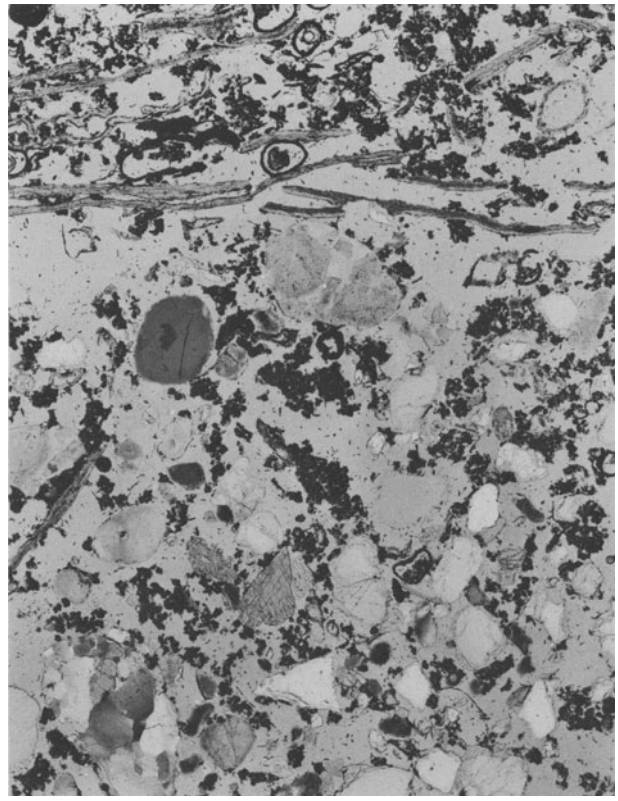

Figure 43. H and A_{hh} horizon of a raw humus. In the H (upper quarter of the picture) of plant residues foliated bark residues still remain; some root residues (occurring transversely, black rings: mycorrhiza mantles) may also be recognized. The A_h has an agglomeratic fabric: flocky to granular, dark small aggregates (loose clusters of droppings of enchytraeids) of organic fine substance between loosely arranged quartz grains. Beech raw humus. (Northwest Germany). Ground thin section (25 μm), half-crossed polarizers, natural size 5.5 mm.

pores are scarcely visible in the 30 μm thin section. The compact forms can be recognized more easily by stereomicroscopic investigation of the thin section; in the microscope only a slightly inhomogeneous distribution of the fine substance is seen in patches of 60 μm in size. Here the pores are about 10 μm in diameter and therefore important for retention of plant-available water. These fabrics up to now have been found in soils with loess-like grain size distribution and with transition forms from mull to moder. In those soils they often comprise more than half of the entire soil material. They are formed by activity of enchytraeids as probably the agglomeratic fabric also.

Spongy fabrics and dropping fabrics in the mineral soil are widespread. A well-developed spongy fabric usually can be found in chernozem and related soils (see *e.g.*, DUDAS and PAWLUK [1969, 1970b], GHITULESCU and STOOPS [1970]). The latter have performed micromorphometric measurements and found an amount of spongy fabric and pedotubules higher than 50% down to 140 cm depth. The humus form of those soils is mull. Small areas of spongy fabric and dropping fabric, however, are found also in the B horizons of other soil types with humus-form moder, which have a denser fabric in the A horizon (BABEL [1972b]); also profiles and microphotos given by KOWALINSKI [1969/70], and PETTAPIECE and ZWARICH [1970] seem to show the same phenomena. At least in some cases they are the remains of a former animal

activity, which has ceased after a change of environmental conditions, especially a change in vegetation by man.

Platy fabrics of the A_h horizon are formed in humus forms that are less favorable in biology (BECKMANN and GEYGER [1967]; Part IV C; Figure 42). An extreme formation found in arable soil was called puff-paste (flaky) structure (DELEENHER [1967]). Other formations are the soil crusts in cultivated soils of the arid and semiarid regions, which show in thin sections a high density and sometimes horizontal fracturing (EVANS and BUOL [1968]) due to non-biological processes of fabric formation — swelling, shrinkage, and frost.

The fabrics quoted show transition formations according to mineral grain size distribution and activity of soil organisms.

In the *covered fabric* (compare KUBIENA [1953]) mineral grains are encased and cemented by organic matter (Figure 45). The covers often show a tangentially layered structure. The innermost layer is brighter in color and consists of material rich in mineral matter; the outermost

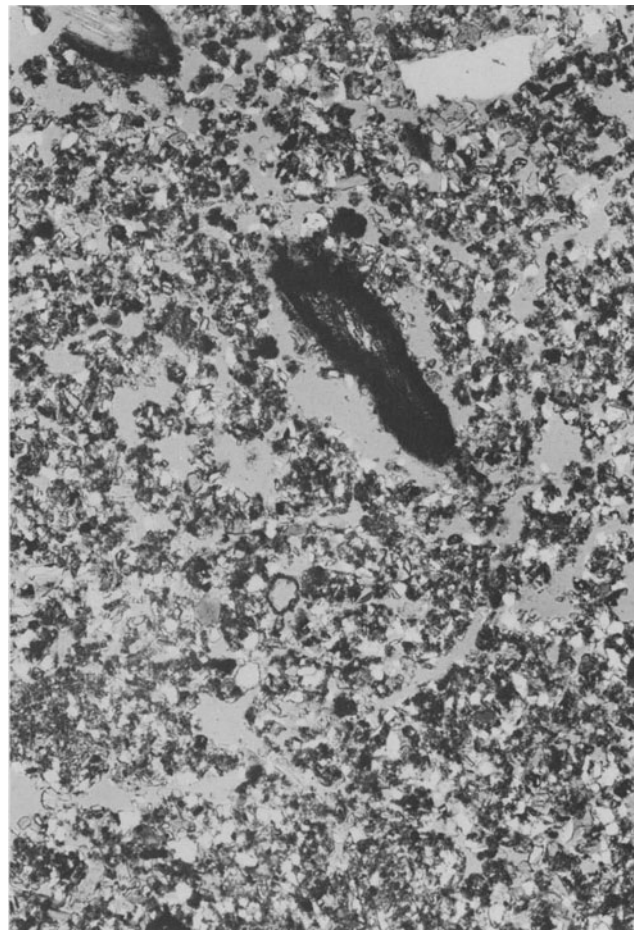

Figure 44. Dropping fabric of enchytraeids, in the A_{hh} horizon of a mull-moder (loess). Above middle to left, loose-lying droppings; above right, little compacted; beside, compacted dropping fabric; below, the droppings are hardly recognizable as primary aggregates in the compacted fabric, in this part some shrinking fissures. (Southwest Germany). Ground thin section (20 μm), half-crossed polarizers, natural size 1.5 mm.

layer is darker and nearly pure organic substance. Shrinkage fissures through the organic layer regularly are found in ground thin sections, but other irregular separations also occur (ALTEMÜLLER [1962a], ALTEMÜLLER and KLINGE [1964]; see also KARPATSCHEWSKI [1960]). This is the fabric of the B_h horizon of podzols. The covers are formed by precipitation of dissolved organic substances washed out from the humus layer (see Part III D 2b).

C. Fabric Classifications

KUBIENA [1938, 1953] describes the fabric formations of humus soil horizons which were known up to that time. He has named some of them (Part IV B). KUBIENA [1970], in part already [1953] names the fabrics from the soil types or the humus forms, for which they are characteristic, *e.g.*, raw humus fabric (for the fabric often found in L_v and F_r, which here is named laminated fabric, Part IV B 1), moder fabric, and mull fabric (for the spongy fabric, Part IV B 3).

This nomenclature has provoked confusion in some cases, as the humus form comprises all horizons of the humus profile, and therefore, *e.g.*, in a moder profile both, a raw humus fabric as a moder fabric may occur.

A systematic description of fabrics of mineral soil horizons is given by BREWER [1964]. But fabric formations caused essentially by organic substances or organisms are treated only incidentally. Brewer's terms "pedotubules" and "aggrotubules" have been quoted above (Part IV A, B). "Fecal pellets" are mentioned as a special group of "pedological features." Only "single fecal pellets" and "welded fecal pellets" are named.

BECKMANN and GEYGER [1967] give a simple classification of the void, aggregate, and structure forms of the mineral soils. There the fabric types of humus mineral soil horizons are taken into account. All quoted "structure forms" ("Spaltstruktur, Fugenstruktur, Bröckelstruktur, Porenstruktur, Schwammstruktur, Krümelstruktur") can occur in humus mineral soil

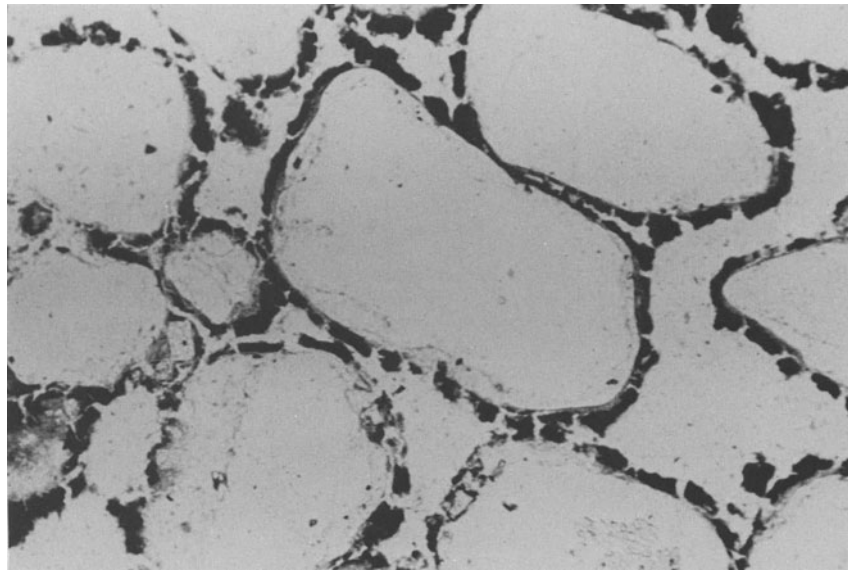

Figure 45. Covered fabric. Quartz grains enclosed by the covers and cemented by them. Inner, brighter cover layer mainly mineral, outer one, organic. Radial shrinkage cracks in the covers. Podsol (from ground moraine). B_h (Northwest Germany). Ground thin section (20 μm), bright field, natural size 0.5 mm.

horizons. The "Krümelstruktur" (= crumb structure) corresponds to a spongy fabric where the aggregates are not combined; it occurs in mull at the surface of the mineral soil. The "Porenstruktur" (= pore structure) corresponds to a compacted spongy fabric, where irregularly formed pores remain; it occurs in the lower parts of the A_h horizon of mull. "Spaltstruktur" (= fissure structure), "Fugenstruktur" (= joint structure), and "Bröckelstruktur" (= fragment structure) occur in humus formations where the nonbiological processes of fabric formation are stronger than the biological ones.

BARRATT [1968/69] proposes a comprehensive classification of microfabrics of humus soil horizons. The criteria of division are the following:

1. skeletal materials ("-skel") or plasmic materials ("-col");
2. organic particles ("humi-"), mineral grains ("lithi-"), organic substance as pigment, bound with clay ("mulli-"), clay ("argilli-");
3. further subdivision according to kinds of tissues or minerals (*e.g.*, "calcitic," "silicic," "lignic," "mycetic");
4. shape of micro structure (*e.g.*, "platy," "pelleted," "spongy");
5. size of particles and aggregates (six classes from "very coarse" to "extremely fine");
6. fabric or arrangement of particles and aggregates.

From this it can be seen that this classification fundamentally is a short description, which has been standardized. Its advantage is that it makes possible a description of all existing microfabrics in a reproducible way. Its disadvantage is that typical fabric formations (typical by morphology as well as by their correlation with certain soil-forming processes) cannot be recognized by nomenclature. A very typical fabric such as the covered fabric is to be termed as humicol-silicic lithiskel complex. While the classification proposed by Barratt can be a useful aid for description of microfabrics, in the cases of well-known typical fabrics, true fabric names nevertheless may be used.

A proposition, taking into consideration the principles of Kubiena, Brewer, Beckmann and Geyger, and Barratt, has been presented by PARFENOVA and YARILOVA [1969].

JONGERIUS [1970] gives a nomenclature for "regrouping phenomena" in Dutch soils, where activities of soil fauna and vegetation are expressed by such terms as "fauna- pedoturbation" (the aggro- and striotubules of BREWER) and "fauna-" and "flora-pedocompaction" (compactions around earthworm channels or roots).

The classification of fabrics of humus soil horizons is still unsatisfactory. One of the reasons is the lack of knowledge about the manifold micromorphology and development of humus profiles.

V. The Micromorphology of the Most Important Natural Humus Formations

The most important terrestrial humus formations were classified by MÜLLER [1887] into three humus forms, which KUBIENA [1953] named mull, moder, and raw humus. These humus forms are defined morphologically. On the basis of micromorphological investigations, Kubiena was able to subdivide and to supplement them. Moreover, he has given short micromorphological descriptions of the submerged and semiterrestrial humus forms, some of which had been first described by VON POST [1862]. Accordingly, the only comprehensive classification of natural humus formations, which is based to a large extent on micromorphological properties, is due to KUBIENA [1953, 1970]).

The following account of the micromorphology of natural humus formations makes use essentially of the differentiation into humus forms given by Kubiena. It is not intended to modify or to supplement this classification. The purpose of this account is not to describe the

system of classification but to describe the micromorphology of natural humus formations. At the present time, moreover, there is not enough micromorphological information material for firmly based changes or supplements, which are certainly desirable in some places.

The term "humus form" is used here as by Kubiena. It always refers to the humus formation as a whole; i.e., by it is meant not only chemical and physical features but, above all, a certain profile structure with all its horizons, its particular internal fabrics as well as the whole of the life in these (KUBIENA [1953, 1955a]). Most humus formations are typified by a special horizon. For raw humus this is the F horizon, or for mull, the A_h horizon. There can also be transition formations, *e.g.*, in terra fusca under forest there is often an F horizon (as found in moder) occurring over the mull (A_h horizon) (KUBIENA [1953]). Still more marked deviations from the typical profile structure can often arise with rapid changes in the environmental conditions. This has induced HARTMANN [1952] to use the term "humus form" for the individual horizons.

A difficulty with the comprehensive appraisal of the literature also lies in the fact that even where the names of humus forms used by Kubiena are employed, there is no complete uniformity in their application. The same is true sometimes for the subhorizon designations, L, F, H. The various authors often do not clearly state how they use these terms (compare, however, BABEL [1971a]).

Other humus classifications that are not taken into consideration here are given by HARTMANN [1952, 1965], HOOVER and LUNT [1962], EHWALD [1956], BARRATT [1964], and WILDE [1971]. Except for Barratt, who gives a classification of grassland humus profiles, they concern forest humus forms. All are largely based on macromorphological features—Barratt and Hartmann on micromorphological ones also.

In recent years some detailed contributions to the micromorphology of peats and of raw humus and moder have been given (see references to Grosse-Brauckmann, Jongerius, Puffe, and Babel). Many other humus forms, on the contrary, have not yet been studied in detail—especially Dy, Gyttja, Sapropel, raw soil humus. Nevertheless, the attempt should be made here to discuss them, at least briefly. (A summary of the micromorphology of humus forms, based on Kubiena, is given by JONGERIUS [1961].)

The following descriptions are based largely on investigations of ground thin sections at low or medium microscopic magnifications. The text, within the individual humus forms, is arranged as follows: general features—micromorphological features (constituents, fabrics)—discussion of the micromorphology with regard to biology and chemistry—different formations (varieties) of the humus form in question.

It must again be emphasized that all humus forms should be defined strictly morphologically. Genetics and dynamics express themselves in morphology, but the connection is known, however, only in a fragmentary manner. Its investigation is plainly the object of morphology. Genetic and dynamic ideas should not therefore enter into the definitions of humus forms. Otherwise an objective, generally valid, basis for the classification of the humus forms will be missed.

A. Nonpeaty, Submerged Humus Formations

The nonpeaty submerged humus formations have as yet scarcely been investigated from the purely soil science side. In his soil systematics KUBIENA [1953] listed the humus forms Dy, Gyttja, and Sapropel. These terms are taken from limnology where they are designations for organogenic sediments (see also the textbooks of limnology).

The use of these terms for humus forms, at least in the case of Dy, is still problematical, since Dy is, as Kubiena himself states, "poor in life to harmful to life" and, therefore, can scarcely be conceived as a humus form. Gyttja, in contrast, possesses a rich fauna and micro-

flora, Sapropel a very specific microflora of putrefaction bacteria. The delimitation of Dy, Gyttja, and Sapropel and their further subdivision is not quite uniform, either in the limnological or in the peat science literature (see a critical survey of the literature by GROSSE-BRAUCKMANN [1961]).

Dy is a macroscopic dark- to black-brown, acid humus formation occurring at the bottom of waters rich in humus, and, according to Kubiena, is characterized micromorphologically by a high proportion of humus gel precipitates. These do not show any regular contours and structures. Larger, pure accumulations of them occur macroscopically as so-called dopplerite. Recognizable plant residues, mainly of sphagnums, also of other mosses and water plants, exist usually only in small amounts; larger quantities characterize transition forms to Gyttja. Of microfossils, predominately sponge needles and diatoms can occur (GROSSE-BRAUCKMANN [1961]). Occasionally chitin residues of aquatic animals are found.

Gyttja is a muddy, organism-rich humus form at the bottom of eutrophic and oligotrophic waters. Micromorphologically it is characterized by numerous microorganisms and their residues, as well as by droppings and residues of droppings of aquatic animals. Recognizable plant residues (coarse and fine detritus of shore plants) can form a considerable proportion. In thin sections the appearance of diatom shells is characteristic. The organic fine substance often shows fissuring in ground thin sections (KUBIENA [1943a]).

The formation can vary in special cases depending on the variety. Von Post (see in GROSSE-BRAUCKMANN [1961]), who in 1862 introduced the term "Gyttja" into scientific usage, distinguished altogether 10 groups, each according to the inorganic impurity, the kind of waters etc. KUBIENA [1953] specified eight varieties. Many of them have an Äfja, an algal layer at the surface, which can contain, in addition to diatoms, especially blue-green algae, but also pellicles of bacteria (KRAUSE [1964]). Mineral components are usually present in considerable amounts; thus in the case of chalk gyttja (KUBIENA [1953]) often large quantities of chalk occur partly in the form of mollusk shells and partly in the form of tiny crystallites less than 1 μ in size.

There are scarcely any investigations based on ground thin sections. Other microscopic investigations were made largely within the framework of hydrobiological and peat studies (for literature, see GROSSE-BRAUCKMANN [1961]).

Sapropel is a blackish to deep-black humus form, which is muddy, partly loose and partly dense. It is formed at the bottom of eutrophic waters under anaerobic conditions and is characterized by the occurrence of hydrogen sulfide and methane. It is produced from about the same starting material as Gyttja. According to KUBIENA [1953], reddish flocks of sulfur bacteria may often be found; droppings of small animals are absent. Occasionally elementary sulfur occurs in whitish-yellow films, but iron sulfide always appears as a bluish-black to black pigment. This often gives rise, on drainage and liming, to the formation of gypsum crystals, which may be recognized microscopically as prisms, pinacoids, lenses, or irregular grains. Sometimes bubble-like pores occur which are produced by the putrefaction gases. There are transition formations for Gyttja, as for Anmoor. Special thin section investigations are lacking.

B. Peats

Here, all peaty humus formations—low moor, transitional, and high moor peats (fen, carr, and moss)—will be dealt with together. In fact their micromorphology is generally very similar. Moreover, the terrestrial humus formations produced by cultivation of peats are relatively independent of the botanical composition of the parent material. Therefore, even in some of the works on the micromorphology of peats it is not clearly stated which kind of peat was investigated. Work can be done on ground thin sections. Often very severe shrinkages

can, of course, interfere. It is better to use sliced thin sections, which offer, in addition, still other advantages. They can be readily prepared also from peat samples in natural arrangement (Cremolan method, see Part VI A 3).

1. *Primary Peats*

Primary peats here mean peats that have not been exposed, through a change in ecological conditions (particularly drainage), to secondary decomposition processes. The description here given is valid for the slightly and moderately decomposed forms mainly investigated hitherto.

As *constituents*, plant parts, many of which can still be identified botanically, can always be recognized with the naked eye (Figure 7; GROSSE-BRAUCKMANN [1963, 1964]). Correspondingly, most peats in thin sections show a large proportion of readily recognizable plant residues. These are sometimes almost colorless (sphagnum residues), usually intensely yellow, brownish-yellow, or brownish-red, and sometimes dark-brown to nearly opaque. Peculiar to more strongly decomposed peats is frequently a striated, juxtaposed arrangement, like nests of brightly and very darkly colored parts of tissue residues (Figure 50) (KUBIENA [1943]). Droppings of aquatic and also of land animals are very rare; in the superficial parts of natural sphagnum peat bogs they occur occasionally (GRACANIN [1962]), similarly also on the underwater surface of sedge bogs (KRAUSE [1964]). In deeper peat layers, droppings were still found by GROSSE-BRAUCKMANN and PUFFE [1964] in individual instances, but only if they had been protected from disintegration by their position in feeding cavities within woody parts, stalks, or leaves.

The same authors found fungal hyphae in places also, mainly in woods and in moss stalks, but also in the fine substance; fungal spores and sclerotia-like formations also occur—these more frequently in high moor than in low moor peats. Besides the droppings, greatly disintegrated material, in which however cell wall fragments are still clearly recognizable, may be found in variable but usually small amounts. In high moor peats it is derived predominantly from the woody and herbaceous plants of the high moor (Figure 7).

As a last group of constituents, homogeneous formations without definite structures should be mentioned (Figure 29). They are characteristic of peats. Often they are more or less fissured, yellow, brownish-yellow, not infrequently very dark to opaque. They often occur in layers, only a few micrometers thick, between the plant residues or as fillings of small spaces. Occasionally, however, they can become visible even macroscopically as dopplerite. They are accumulations of humus substances separated from the solution phase. These formations are, in part, not distinguishable with certainty from more or less topochemical transformation products of plant residues, which are recognizable only by the contours but no longer by the internal structures; such pictures can be presented, *e.g.*, by residues of cotton-grass-leaf sheaths (Eriophorum). Moreover, sometimes, as GROSSE-BRAUCKMANN and PUFFE [1964] have likewise shown, in dark parts seeming at first to be quite homogeneous, a still considerable proportion of well preserved but strongly disintegrated cell wall fragments may be recognized with the polarization microscope. In such forms it may be assumed that dissolved humus substances have precipitated in and between the still-intact structures.

The *fabric* that is built up from these constituents is determined by the high proportion of rather large plant residues. These form a laminated skeleton whose interstices are partly more, partly less filled in with finely divided residues and with homogeneous humus accumulations. In fresh, water-saturated peats the latter can thickly envelope the plant residues. In thin sections they are often shrunken characteristically so that cracks are added to the natural pore spaces. In slightly decomposed peats these humus portions without definite structures, form only, in places, thin horizontal layers (not more than 10 to 20 μ) between the plant residues.

As to the *decomposition of the plant residues* in primary peats, something more can be added from the works of GROSSE-BRAUCKMANN [1963, 1964] and GROSSE-BRAUCKMANN and PUFFE [1964].

The phenomena are, in principle, similar in high and low moors, although in low moors many plant species are decomposed until they are unidentifiable, depending on the more eutrophic conditions.

Sphagnums are preserved the best; they usually show distinct decomposition symptoms only in the stems (KOX [1954]). Herbaceous and woody plants, on the contrary, are considerably more strongly decomposed. Of these, the best preserved are subterranean shoot parts; the aerial parts are the worse preserved the drier the local site on which the plants in question are growing. Thus in peats of northwestern Germany, for example, leaves of the very common *Calluna vulgaris* are much more scarce than their basal stem parts and roots. The most easily decomposed tissues are generally parenchyma, followed by lignified tissues, although these are readily consumed by animals; barks and the outer parts of cortex and epidermis are the best preserved. This sequence corresponds exactly with the findings of plant residues in terrestrial humus forms (for details see Part III B). The degradation of cellulose, detected by double refraction, often parallels the decomposition of the structures. But there are also apparently not infrequent instances in which quite well-preserved structures no longer show double refraction. This, according to the author's observations, however, cannot be taken as in fundamental contrast to the conditions in the case of terrestrial humus forms (BABEL [1964]) (see also Part III).

On the whole it follows from these microscopic investigations, in agreement with already known notions, that the primary chemical properties of particular parent materials, on the one hand, and the anaerobic conditions, on the other, are the decisive factors leading to peat formation. Animals and fungi do not play any essential role. (Nothing can be said of the importance of bacteria, since they have not yet been made visible in peat thin sections.) A larger proportion of humus substances than with terrestrial humus formations is moved in solution and, on precipitation, forms fabric constituents of its own. Where, under dystrophic conditions the precipitated substances form continuous pure layers at the bottom of the waters, the formation of Dy is involved (see Section V A). No precise statement can be made as to the extent of the mineralization which, in addition to the removal of decomposition products in solution could have caused the complete disappearance of many tissue parts. The high values for the mineralization, which have been determined from comparisons with the dry matter production of living moors up to 80% (HOLLING and OVERBECK [1961]), could by no means have been expected, however, from the microscopic picture.

KOWALINSKI and KOLLENDER-SZYCH [1960] tried to characterize peaty muck soils by micromorphological analyses of constituents of humus and by chemical methods. They grouped the constituents into different groups according to BABEL [1965b].

2. *Secondary Humus Formations from Peats*

The decomposition and humification processes, which are promoted by drainage and cultivation of moors, may be followed very well micromorphologically. The account given here is based essentially on the works of PUFFE and GROSSE-BRAUCKMANN [1963], FRERCKS and PUFFE [1964] and JONGERIUS and PONS [1962a, b]; numerous illustrations may be found therein.

The increase in droppings is particularly striking. Feeding cavities with mite droppings may often be found down to a depth of some decimeters in sphagnum stems, in the stem bases of Eriophorum, in woody Ericaceae residues, and similar places. It may be very beautifully observed how first the thin-walled and later often nearly the whole material is converted into droppings, which remain well preserved in their egg-shaped contours for some time. Only the

very resistant tissues usually remain behind undisintegrated. Similarly in Gyttja muck soils droppings have been found revealing recent biological processes (UGGLA *et al.*, [1969]). In addition, fungi occur both in the nondisintegrated plant residues as well as in the droppings and their breakdown products. Sclerotia also are frequently found. The decomposition of the droppings and the tissues decomposed by fungi lead to an enrichment of very fine-particled fine substance. This can become very dense, especially when formed by fungal degradative activity, and it tends to produce shrinkage cracks (PUFFE [1965]).

Intact tissues in secondary decomposed peats are often much darker than in primary peats; they can commonly appear opaque in 30 μm thick sections. Also, droppings can darken until opaque. Structureless substances, which likewise are very dark to opaque, are more frequent than in primary peats. In the subsoil they are often enriched (B horizon) and, as thick masses, surround the still quite well-preserved plant residues (JONGERIUS and PONS [1962a]).

According to JONGERIUS and PONS [1962a]), in Dutch moors microbiological transformations at first go on side by side or after physical "maturing processes," which are not described micromorphologically. The easily decomposable plant substances, such as pectin, cellulose, hemicellulose, and proteins are broken down; their humification products, which go into solution, are thought to cause the black color of the still-intact plant residues. Degradation by soil animals ensues usually only after this phase, but it is still accompanied by microbiological transformation processes. The droppings decompose, especially in the nutrient-poorer formations, after a short time.

On the whole, a humus form is thus produced which is related to moder. However, since the substrate—namely peat—is situated *below* the main sphere of action of the decomposition agents, it shows a fermentation layer that lies under the humus substance layer. From the top downward, however, organic material is likewise supplied by the living plant cover, so that one obtains also, as usual, above the humus substance layer, a fermentation layer. Thus there

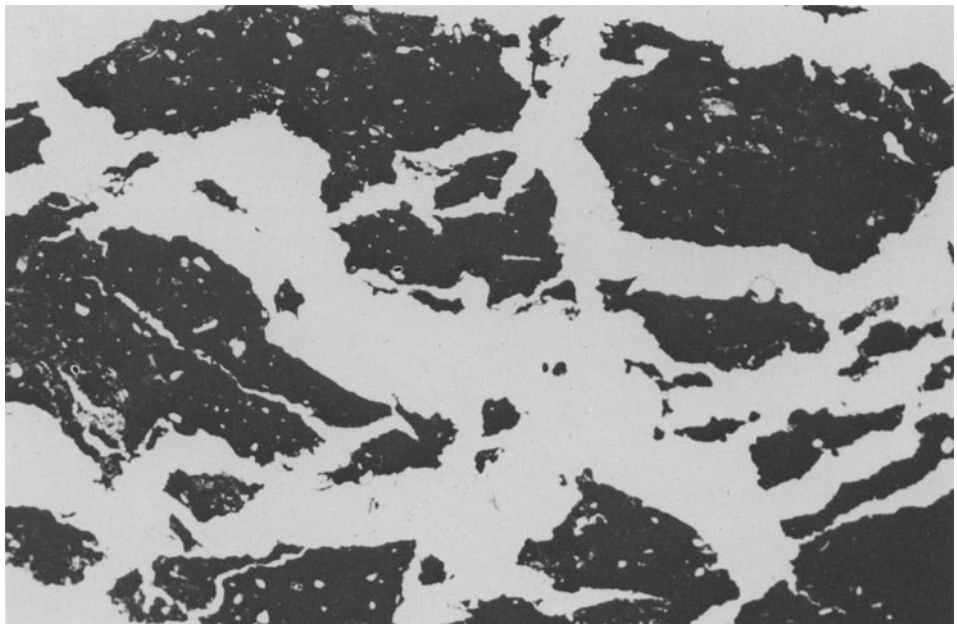

Figure 46. Pitch peat (strongly decomposed peat moder). Sharp-edged, dark aggregates with few plant residues. Cultivated peat over gley (South Germany). Ground thin section (20 μm), bright field, natural size 1.5 mm. (From a preparation by L. Menge, Stuttgart-Hohenheim.)

develops an L – F – H – F profile, as PUFFE and GROSSE-BRAUCKMANN [1963] and FRERCKS and PUFFE [1964] have shown in the case of drained high moors.

Under arable land the profiles of moder-like formations from peats are frequently characterized, in addition, according to JONGERIUS and PONS [1962a], by an organic B horizon which is formed by separations of dissolved humus substances migrated downward from above. In arable cultivation strong decomposition processes promote an unfavorable further development of peat moder, which is known agriculturally in German as "Vermullung," and which results in formation of pitch peat (KUBIENA [1953]) (Figure 46). It consists predominantly of fine substance, which forms a very dense fabric, which, on drying out, breaks down into hard, sharp-edged, scarcely wettable aggregates, which are deep brown.

According to JONGERIUS and PONS [1962], with larger proportions of mineral material and favorable physicochemical conditions but independently of the botanical composition of the peat, the development follows another direction. After similar initial stages, earthworms appear as secondary decomposers, and lead to the formation of a more or less stable spongy fabric, as is characteristic of typical mull. The lower parts of the profile can still have the characteristics of moder. This mull however always contains dark to opaque constituents, 25 to 50 μm in size, in the brown ground mass. As a rule, they exhibit plant structures, although some of them are without structure. The smaller the number of these inclusions, the more favorable seems to be the mull formation, as comparisons with agricultural experiences have shown. Peat-like moder formations also have small opaque constituents, as a rule (observations of the author; also HARTMANN [1952]; see also the following section on Anmoors).

Secondary humus formations from peats sometimes show transitions to Anmoor.

C. Anmoor

According to KUBIENA [1953], Anmoor is a gyttja-like humus form, produced under the temporary influence of ground water or back water. It is dark grey to blackish and has an inky smell. In the wet state it is muddy; in the dried condition it is transformed into an earthy fabric. The English term "Fenmull" appears to be synonymous with Anmoor (MADER [1953], EHWALD [1956]).

The micromorphological description is based on the works of KUBIENA [1953], JONGERIUS [1961], and KOWALINSKI [1964a, b]. Investigations of the aggregate fabric of Anmoor were made by MENGE [1965].

Plant residues do not usually play any quantitatively significant role as *fabric constituents* of the Anmoor; they are dull brown, dark brown, or opaque. Very dark or opaque plant fragments seem, in general, to be typical of humus formation under water or, at least, severe intermittent wetness (see also Figures 14, 16; also ALTEMÜLLER [1960]; this is true also for peats; Figure 50).

Fine substance is present among other things, in the form of strongly humified dropping material. The original dropping forms are usually no longer preserved. In addition, part of the organic substance always occurs in holorganic homogeneous bodies without definite structures. From these Anmoor resembles peats and nonpeaty submerged humus formations. This material can be developed in some Anmoor formations as illuviation cutans which cover pore walls and exhibit flow structures (JONGERIUS and JAGER [1964]). The cutans generally contain tiny opaque granules, scarcely more than 1 μm in diameter. Sometimes the cutans consist completely of opaque material.

Diatom shells are a characteristic feature present. Mineral matter is present in varying amounts. Often fine iron precipitates or iron concentrations occur as encrustations on roots. In some formations related to sapropel, gypsum crystals may be found as new formations.

Variations in hydrological conditions produce variations in *fabric*. Under the original semiterrestrial conditions a rather dense fabric usually forms, but if terrestrial conditions arise, a crumb fabric is formed. On the whole, dull and dark colors are dominant. According to JONGERIUS [1961], within the inner fabric gradually merging color transitions from very light brown to very dark and to opaque regions are typical (Figure 49). Mineral grains are loosely arranged. In organic B horizons, however, above all under plough land, the mineral grains are surrounded by black, homogeneous, often fissured, humus material. These results of *Jongerius*

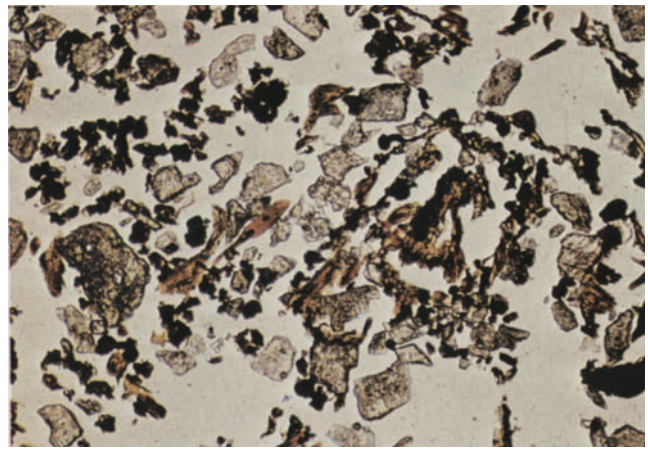

Figure 47. Rendzina moder, A_h horizon. Reddish-brown plant residues, predominantly of mosses. Organic fine substance particles (dropping residues) dark to opaque. Calcite grains. Loose arrangement (central uplands of Germany). Ground thin section (35 μm), bright field, natural size 1.2 mm.

Figure 48. Tangel layer. The dark-colored fine substance which surrounds the needle residues, originates from earthworm droppings. It contains in part holorganic, in part mineral particles of sand and silt fraction (quartz, mica, calcite). The small, longish, brown particles are needle fragments. All the plant residues are of *Pinus mugo* needles. Above, right-hand side, a needle with well-preserved mite droppings; below that, a needle with densely lying residues of decomposed droppings; below, a needle, length-wise, with two fungal congestion zones. *Pinus mugo* tangel, F_rA_{hh} horizon (Alps). Ground thin section (30 μm), bright field, natural size 4 mm.

have been obtained from Anmoors secondarily subjected to terrestrial conditions; Jongerius' definition of Anmoor is undoubtedly not completely identical with that of Kubiena.

In wet raw soils of the arctic regions KUBIENA [1970], found very typical "mud coatings,"

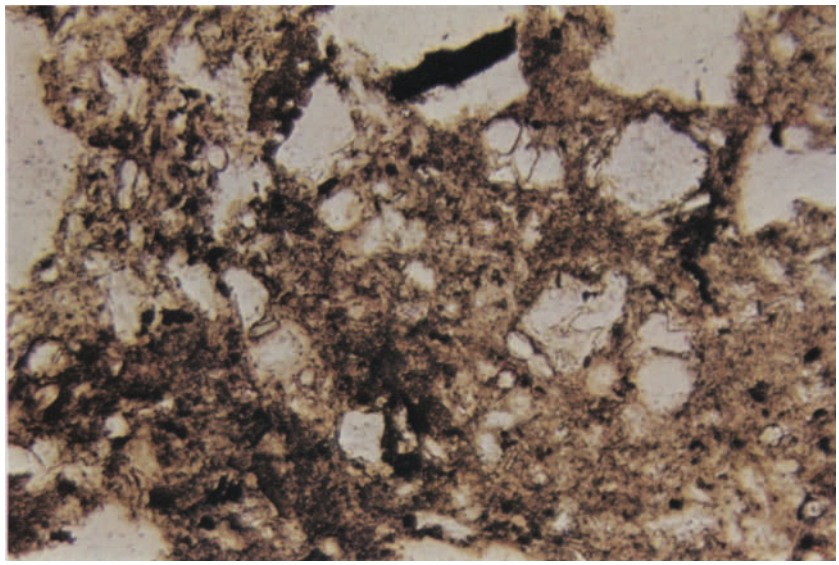

Figure 49. Anmoor. From the mineral fine substance, some organic fine substance particles stand out dull brown, dark brown, or opaque. Gradual color transitions in the mineral fine substance (larger quartz particles appear like holes in the fine substance). A_h (3 cm) (German Baltic coast). Ground thin section (15 μm), bright field, natural size 450 μm.

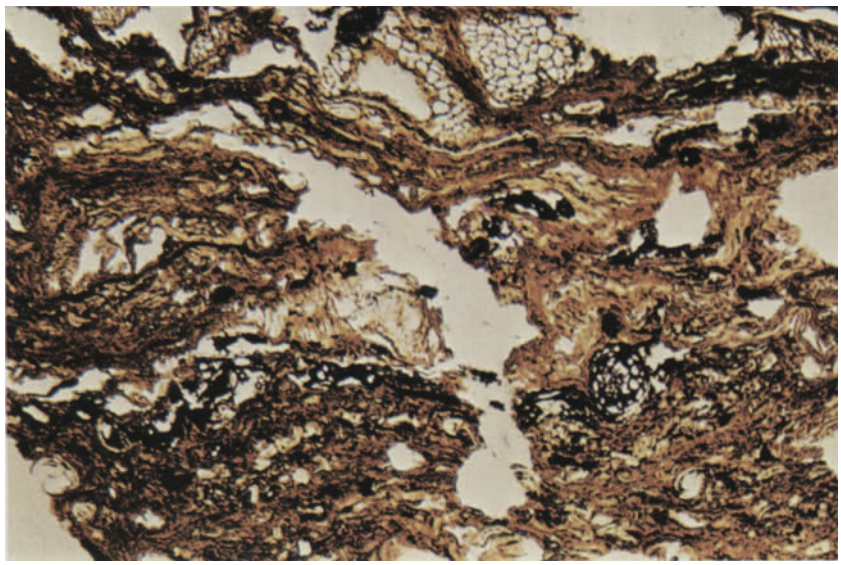

Figure 50. Strongly decomposed peat. Top, easily recognizable tissues; the majority of the plant residues compressed in bands; some nearly opaque bands and groups. Carr (wood peat, 25 cm) (Black Forest, Germany). Ground thin section (15 μm), bright field, natural size 1.1 mm.

which encase soil aggregates and isolated sand grains and which sometimes are very rich in humus, which has precipitated from the soil solution.

The dark-colored aggregates are usually very rich in iron, according to chemical studies by KOWALINSKI [1964a, b], so that this author speaks of aggregates of a silica-iron-humus type, which he contrasts with lighter-colored aggregates of a silica-aluminium-humus type.

The *variety* of Anmoor that develops depends on the amount and nature of mineral constitutents and upon hydrological conditions. Dystrophic varieties related to peats have a higher proportion of plant residues. Anmoor can pass over into Gyttja or into mull under certain hydrological conditions.

D. Terrestrial Humus Formations

1. *Raw Humus and Moder (Silicate Moder)*

The two most important terrestrial superficial humus forms, raw humus and moder, have many properties in common. In English and American classifications they are, therefore, grouped into one single humus formation mor (*e.g.*, HOOVER and LUNT [1952]).

Above all, both show macroscopically the characteristic horizon sequence (cf. Section II C): litter (L layer), decay layer or fermentation layer (F layer), humus substance layer (H layer). This humus profile represents the successive stages of decomposition of the litter (BABEL [1971]).

There is a principal theoretical difference between raw humus and moder. Fungi are dominant in the decay layer of raw humus, while soil animals are dominant in the decay layer of moder. Micromorphological investigations have often shown that this is only a quantitative difference. The definition of the two forms is not given by this genetical difference, but by differences in the macromorphology of their profiles. Transitions between the two forms, however, often occur. They have been investigated in the classical work of MÜLLER [1887] but further comparisons are needed.

(a) Common Properties

The *litter layer* (L) consists of macroscopically slightly changed, only browned, loose-lying plant litter, mainly from leaves or needles. The parenchymatous tissues in them are browned, the others unchanged. Fine substance is present in only minimal proportions (in the L_n of a moder were found 2%, in the L_v 13% (BABEL [1971a]). It exists mainly in the form of a dark deposit on the surfaces of the leaves. This often consists chiefly of very dark to opaque droppings of collemboles and enchytraeids, which may sometimes accumulate in the lower part of the L layer (ZACHARIAE [1963, 1964], BABEL [1964b]).

In the *decay layer* (F) the residues of fine roots occur in addition to fragments of leaves and needles (Figure 1). They occur in very high amounts preferably under ecologically unfavorable conditions (for quantitative assessments see MEYER [1967]; see Figure 12). Leaf residues are more or less disintegrated. Changes, which point to chemical alterations, do not ensue at the same time as the mechanical disintegration, however, but usually occur later and gradually (for further details see Part III B and C). Most of the tissues in the upper parts of the decay layer are still readily recognized microscopically and as a rule easily interpreted. Their structures, however, are somewhat distorted. In addition to the parenchymatous tissues, the lignified tissues gradually become browned. Yellow, brownish-yellow, and brownish red colors predominate in the transmittent light. In the lower part of the F layer most of the parenchymatous and the lignified tissues are destroyed and phlobaphene-containing tissues (see Section III B 2 c α), are enriched.

Fungal hyphae are always to be found. They are usually stout-walled with a characteristic dark brown color. They grow most frequently on the surface of the leaf residues, but they are also found in the interior of the tissues. In addition, they occur in the fine substance, usually as small fragments. Frequently present are deep brown plectenchyma, which are opaque in places and ring-shaped in cross section. These are mycorrhiza mantels. The roots that were surrounded by them are often decomposed completely or to small residual amounts (Figure 21).

Droppings and dropping residues increase toward the lower parts of the decay layer. They are still often well preserved in their characteristic contours. This is particularly the case when they lie in feeding cavities that are frequently found in pieces of wood and in needles. Their color, as a rule, is that of the parent material. Free-lying droppings are often eaten again by other animals. If that is not the case, they sometimes fall apart only slowly (ZACHARIAE [1965]). This is true especially under dry conditions (RIGHI [1969]).

In the fine substance, in addition to fungal hyphae and dropping material, there are tissue and cell fragments left behind after the partial destruction of the tissues by fungi or animals. In debris preparations of the fine substance one occasionally finds chitinous parts of animals (MÜLLER [1887]).

The *humus substance layer* (H) is macroscopically black-brown to nearly black. Plant residues become rarer. These are mainly the residues of roots; sometimes residues of barks and leaf stalks occur (Figure 43; (BABEL [1972b]). In the phlobaphene-containing tissue residues, occasionally a blackening of the cell content substances may be observed (BABEL [1964b]). Sometimes also, the whole plant residues appear blackened as though carbonized; but the plant parts are structurally still well preserved (PARFENOVA and YARILOVA [1960]).

In the fine substance of the H layer, which consists mostly of the same consituents as those of the F layer, a darker coloration is usually shown than in that of the F layer. In thin sections dull and dark brown colors are predominant (compare RIGHI [1969]). Very small bright-colored tissue fragments occur occasionally. The fine substance is not homogeneous. Under stronger magnification, it still shows considerable amounts of cell wall fragments, which are enclosed in the browned, irregular granular flocky mass and which often become visible only by fluorescence illumination (Figures 24, 23, 22; for more details see Part III C 2). In unfavorable moder forms ("dysmoder") gelatinous accumulations of the browned granular masses were observed (DELECOUR and MANIL [1962]). In some, especially much wetter forms, fragments of fungal hyphae are numerous. They can constitute about half of the whole material (Figure 21) (ROMMELL [1955]). Frequently sclerotia may also be found (BABEL [1964b]); where they occur in large amounts, the microfabric is termed "sclerotial phase" by BARRATT [1968/69]. Finally, single quartz grains may be found.

The *mineral humus horizon* (A_h) is usually very dark black grey, or black brown. When the mineral matter is sand, it contains the same organic constitutents as the fine substance of the H layer (Figure 43). In the lower part of the A_h horizon the organic particles are brightened appreciably (BAL [1970]).

The *fabric* in the decay layer is composed of plant residues as a skeleton and the fine substance. The fine substance is deposited partly in separate, small, loose aggregates, and partly in larger, looser or dense masses between the skeleton. In ground thin sections one still observes many voids. Plant residues become rarer in the lower decay layer. They are often included in the fine substance of this layer.

In the humus substance layer exists a more or less dense fabric. It is usually fissured in ground thin sections. It is formed by the fine substance combining to give larger aggregates. But often a dropping fabric can be observed also.

In the mineral humus horizon (A_h) an agglomeratic fabric is usually formed. Occasionally

brown fungal hyphae can be found as binding materials between the sand grains (BARRATT [1962], BURGES [1963]).

Traces of microbial and animal degradative activity occur particularly in the decay layer. The complete disappearance of whole tissue parts generally indicates microbial decomposition. With animal decomposition, droppings remain behind, which, in raw humus, frequently come from mites and enchytraeids. In addition to these in moder, many other animals are present.

The organic material that is present, especially in moder, enters the mineral horizon (A_h) mainly by particles being washed in with rain water. Part is also transported into the A_h horizon in the dissolved form (JONGERIUS [1961], HARTMANN [1952]). This, however, cannot be observed micromorphologically for certain. An indirect indication of the movement of dissolved organic substances in the poorer forms is the occurrence of uncovered quartz grains (KUBIENA [1953]). As to an indication of a chemical change of the organic substance by admixture into the A_h horizon, see Part III D 2b.

In BABEL [1972b], who has investigated a range from a raw humus-like moder to a mull-moder, the profile is subdivided into eight horizons. Their definition is macromorphological. Their dynamics has been concluded from macromorphological to micromorphological investigations. In the following the *processes* are quoted at those horizons, where their effects become visible.

L_n (definition: litter without macromorphological decomposition phenomena). Very low abiological disintegration and chemical alteration. Loose fabric, still moved by the wind.

L_v (definition: marked macromorphological alterations of the litter, but nearly without fine substance). High solution processes and microbiological actions. Formation of a laminated fabric.

F_r (definition: plant residues are predominant, low content of fine substance). High activity of primary decomposer animals. Breakdown of the laminated fabric. Penetration of roots.

F_m (definition: ratios of plant residues and fine substance are about the same). Further activity of primary decomposers, activity of secondary decomposers, resulting in high disintegration of plant residues. Beginning development of a fabric formed by fine substance only. Highly penetrated by roots.

H_r and H_f (definition: organic fine substance predominant, H_r (few) and H_f (no) above ground plant residues). Horizon with low decomposition processes. Further activity of secondary decomposers. Enrichment of plant substances which are resistant to decomposition and of newly formed stable substances. Dropping fabric or dense fine substance fabric.

A_{hh} (definition: upper part of the A_h horizon, very rich in humus). The horizon is formed by all sorts of blending processes. With exception of the high content of mineral material, only small changes in comparison to the H horizon. Low increase of chemical processes.

A_{hu} (definition: lower part of the A_h with lower humus content). Blending of organic substance only in solution form or by roots. Low turnover of the organic substance and very low animal activity. Droppings are sometimes enriched and form dropping fabric.

(b) Raw Humus

For the differentiation of raw humus from moder, the great thickness of the decay layer is decisive (KUBIENA [1953]). (In the literature written in German humus layers with a thick and dense H horizon often are also termed raw humus; here, however, the term raw humus is not applied for those humus formations.) Within the decay layer, the upper part predominates. It is composed predominantly of scarcely disintegrated but often soft or delicate and densely lying plant residues. They form a laminated, sometimes matted cover. Biologically, this profile formation involves low activity of the decomposing organisms, especially of the animals.

Special groups of fungi are capable of living in the frequently severely desiccated upper decay layer (MEYER [1964]).

Raw humus is produced from a vegetation, the litter of which is poor in nitrogen and rich in thick-walled tissues.

Among the plant residues of the *decay layer*, fine roots and their residues play a very big role, in addition to the material coming from the litter. The fine roots form a dense reticulum that permeates the remaining material. The root residues are preserved for a long time (MÜLLER [1887]). From microscopic investigations of the plant residues, the complete disappearance of whole tissues is often shown, which indicates fungal degradation. These phenomena, which are dealt with in more detail in Section III, occur also in other humus forms. In the upper F layer of raw humus, however, they indicate the only severe decomposition process. More precise investigations on the morphology of fungal degradation in raw humus are lacking. A part of the leaf parenchyma remains long preserved, however, in the browned state until disintegrated by animals.

In the fine substance of the decay layer brown fungal hyphae are common. MÜLLER [1887) describes three morphologically distinguishable groups. According to MEYER [1964], *Cenococcum graniforme* (Sow.) Ferd. et Winge, belonging to the fungi imperfecti, plays a significant role in raw humus formations, in northwest Germany. Strong development of an aerial mycelium penetrating the pores seems to occur particularly frequently in the upper F layer of fairly dry raw humus formations (Figure 32).

Droppings appear in the F layer in only small amounts, but they occur in all raw humus formations. The strongly disintegrated material, which remains after the droppings have fallen apart, is often not distinguishable with certainty from disintegrated residues from fungal decomposition.

In the *mineral humus horizon* (A_h) the quartz grains are without coatings. This is an indication of percolating dissolved humus substances. Precipitates of these cannot be recognized. (The humus illuvial horizon of podzols, B_h, showing such precipitates does not belong to the humus form raw humus. It often does not occur under raw humus. It is discussed in the treatment of the organic matter in the mineral soil horizons in Section III D 2 b.) Roots are normally very rare in the mineral humus horizon of raw humus.

The *fabric* of the upper decay layer (F_r) is determined by the laminated arrangement of the slightly disintegrated plant residues. These are bound by occasional bridge-forming fine substance aggregates, a great part of which is derived from enchytraeid and dendrobaena droppings (ZACHARIAE [1965]). The formation of solid felts, often striking in the fields, is caused by fungal hyphae, which in some forms can render the material matted and breakable, even in the F_m layer and in the H layer. Other differences in the fabric of the deeper horizons of moder and raw humus are not known for certain.

The *decomposition* of the plant residues is carried out mainly by fungi in the characteristic upper decay layer of raw humus. Animals also participate in the decomposition in the lower decay layer. The thickness of the decay layer shows that the processes take place slowly.

In the raw humus profile there are some *variations*. In the extreme case the F layer can become very firm and densely matted, while the H layer is nearly absent. This variety was earlier designated as "Auflagetorf" (peat humus) in the German literature (VATER [1904]) quoted after KUBIENA [1953]). This misleading term should not be used.

(c) Moder (Silicate Moder)

Litter, decay layer, and humus substance layer are about equally thick in the typical moder (KUBIENA [1953]). Often, however, litter and decay layers decline very markedly in comparison with the humus substance layer. The latter is often very rich in sand, so that in some cases in

its whole depth it is more properly designated as a mineral humus horizon (A_h). In other formations, H and A_h are clearly distinguished, however, even though the boundary is not so sharply demarcated as with raw humus.

The *decay layer* consists of dropping materials and plant residues, whose particles are usually smaller than in raw humus. Only a moderate proportion of the plant residues are fine roots, in contrast to raw humus. Fungal decomposition of the tissues may also be observed here (MEYER [1962]). Brown fungal hyphae are regularly found but rarely in large amounts. Often various kinds of dropping forms suggest the occurrence of many species in the fauna. Quantitatively, droppings and dropping residues regularly are very prominent (Figure 1). MÜLLER[1887] reports that chitin residues of arthropods can often be found in the decay layer.

The *humus substance layer* shows no clear differentiating features in contrast to that of raw humus.

The *mineral humus horizon* can be very thick in sandy soils. In such formations JONGERIUS [1961] observed increasing dark coloration of the organic fine substance down to about 20 cm deep, but between 20 and 40 cm a color change to lighter brown and sometimes yellow. Still further down, the small organic aggregates fall apart completely and their residues settle on the mineral soil skeleton. Jongerius interprets these phenomena as the results of gradual mineralization (compare also the detailed study of BAL [1970]). In contrast to the same horizon of raw humus, the A_h horizon of moder contains varying amounts of roots.

The *fabric* of the F layer of moder is not matted and laminated as in raw humus. Fungal hyphae are not numerous but droppings are very numerous, which indicates that animals are very important in promoting disintegration of the plant litter. Collembola, enchytraeids, small earthworms (SCHALLER [1950], DUNGER [1956], ZACHARIAE [1963, 1964], VAN DER DRIFT [1964]) and insect larvae play a large role in these disintegration processes. According to ZACHARIAE [1967], in spruce forests Tipulidae larvae often are the primary decomposers of litter. In profiles richer in mineral nutrients, isopods and diplopods are also important.

Animals do participate in the transport of organic matter into the mineral soil horizons (JONGERIUS [1961]) to a very small extent and distance only (a few millimeters). Above all

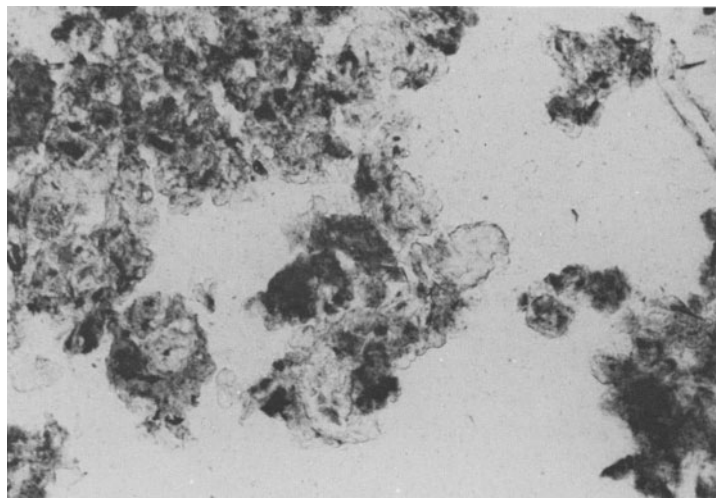

Figure 51. "Swollen moder" (see Barratt (1964)). Organic fine substance (partly with residues of tissue structures) appearing swollen (perhaps an artifact that is characteristic of some wet moder formations). Wet moder with transition to peat formation, H (Black Forest, Germany). Ground thin section (20 μm), bright field, natural size 450 μm.

they effect a closer intermingling of the organic and mineral matter (*e.g.*, *Lumbricus rubellus*; see ZACHARIAE [1965]). Infiltrating of rain water was shown by VAN DER DRIFT [1964] to be largely responsible for the transport of organic matter from moder formations into lower sandy horizons. There, the organic particles in the A_h horizon often form horizontal bands, which may be interpreted only as an infiltration type of action.

Moder is much commoner than raw humus. It is the most widespread humus form of the forests of temperate climatic regions. There is a great deal of *variation* in silicate moder. MÜLLER [1887] and VAN DER DRIFT [1964] have done the only micromorphological comparisons of different varieties. Fluctuations in the thickness of the F and H layers and in the degree of disintegrations of the plant residues in the F layer can be seen macromorphologically. In the German literature the rather unfortunate terms "coarse" and "fine" moder have become established (KUBIENA [1953]), wherein coarse moder (according to DELECOUR and MANIL [1962]: dysmoder) resembles raw humus.

BARRATT [1964] mentions as a special "microfabric" a "swollen moder," which is formed at sites with temporary severe wetting. The structures of the fine substance appear swollen in thin sections. This impression is caused by a very light, lobular margin, sharply demarcated against the embedding medium. However, these structures may be artifacts which could just as well be typical of wet moder forms (Figure 51).

2. *Rendzina Moder*

Rendzina moder is the humus form of shallow soils on chalk or limestone (protorendzinas (KUBIENA [1943b, 1953]). It is a fine, macroscopically black moder, usually lacking a coherent decay layer.

A small proportion of disintegrated plant residues may be recognized microscopically in the H layer. These are often colored dark brown and their tissues are still rather well preserved. They often show traces of feeding. The main characteristic constituents are droppings showing well-maintained forms or only a partial breakdown. Their black color is the most striking characteristic of rendzina moder (Figure 47). In transmittent light they are opaque in the thicker places of thin sections. In the thinner places they are grey, brown, or colorless, and densely covered with opaque small-grained substances (calcium humates). Fresh droppings may be recognized partly by their shining brown colors; however, they appear to darken very quickly. In addition usually small calcite grains occur in varying amounts.

These constituents form a very loose *fabric*. Rarely, the droppings are slightly agglomerated. Aggregates of a higher order are never formed. Parts of the dark fine substance often encrust the clearer plant residues and the lower stem parts of living moss cushions. The calcite grains are not associated with other constituents. Because of this fabric, the whole humus formation is more or less dusty in the dry condition. KUBIENA [1938], described the fabric as rendzina fabric. The traces of feeding and the droppings originate from oribatids, probably partly from enchytraeids (ZACHARIAE [1964]).

3. *Alpine Pitch Moder*

This is the humus form of the alpine pitch rendzina (Alpine Pechrendsina [KUBIENA 1953, 1970]). It is formed at the alpine level under natural grassland on limestone, but is completely free of lime. While a decay layer is usually scarcely formed, the humus substance layer is more than 20 cm deep. The upper part (H_1) is strongly penetrated by roots, and it is rather loose, fine-crumbed, and blackish brown. The lower part (H_2) is dense, prismatically breakable, nearly black, and macroscopically homogeneous (see profile descriptions in SOLAR [1960]).

In the typical formations larger plant residues are found only in the H_1 layer and even there in small amounts. On the contrary, very small plant residues (100 μm and below) can be

found in small or moderate quantities throughout (Figures 25, 40, and 41). They are usually reddish brown and often may be identified as residues of root cortex. The main quantities are a dirty brown, blackish brown in 30 μ sections, or reddish brown in thinner sections, very fine-particled material, which, in some pitch moder formations, is clearly formed as 30 to 50 μ large cylindrical droppings. This material consists of irregularly formed, strongly colored substances, partly with granular internal structures in which smaller amounts of difficult to recognize cell wall residues are included (Figure 25) (observations of the author). Under crossed polarizers the cell wall residues are visible by double refraction. Hyphae are rare. Calcite is lacking, quartz of aeolic origin is often present in small to moderate amounts.

The *fabric* appears moderately loose to moderately dense in thin sections. Between the small loosely cemented droppings a fine-pored space system remains free (Figure 40). A similar fabric is formed in other cases in which the primary aggregates show no clear dropping forms, but are irregularly delimited and loosely cross-linked with each other. In sections of the H_2 layer, shrinkage cracks always appear (Figure 41). The droppings most probably are produced by enchytraeidae (presumption of ZACHARIAE [1964] because of their great resemblance to enchytraeidae droppings in moder), in part perhaps also by collembola, which often occur abundantly.

According to KUBIENA [1953, 1970], pitch moder develops from rendzina moder under humid conditions by dissolution of the lime. There are dystrophic varieties, which contain more plant residues and more fungal hyphae and sclerotia.

4. *Mull-like Moder*

This humus form occurs especially in soils with advanced physical but slight chemical weathering and under grassland vegetation. It is very similar to mull macroscopically. It is characterized by the capacity for forming rather large aggreagtes. A true mull formation is not brought about, however, because of the lack of clay (KUBIENA [1943b, 1953]). Differentiation from mull is sometimes possible only with the help of the microscope. An F layer is seldom formed and an holorganic H layer is absent.

The mull-like moder of KUBIENA [1953], to which the humus formations described here should be assigned, probably frequently corresponds to the fine mull of HOOVER and LUNT [1952]. It is a true humus form and not a complex formation ("twin" formation) of moder and mull. In contrast, the mull-like moder of HARTMANN [1965] (see also EHWALD [1956]) is closer to the twin mull.

On microscopical investigation, plant residues can scarcely be found in the A_h horizon. The organic substance occurs almost entirely as a very fine-particled material which is similar to that in the H layer of moder. In addition, a high proportion of mineral grains of the sand fraction and predominantly of the silt fraction is always present (Figures 52, 53, and 26).

The *fabric* is characteristic. The organic fine substance particles are very intimately mixed with the mineral fine substance. Both components, which can be readily separated from each other microscopically, are contained in droppings, which are present in various formations and usually in sizes above 0.5 mm. They are evidently quite stable. Locally, nearly the whole fabric is composed of droppings.

The intimate mechanical mixing of organic and mineral substance is due to a rich soil fauna. These animals consume mineral material together with the organic food. These are julids, glomerids, insect larvae, small earthworms, and enchytraeids. Soil biological and electron microscopical studies by SZABO *et al.* [1962] and SZABO *et al.* [1964] show the morphology of the dropping and of the plant microorganisms, which mostly appear to be colony-forming.

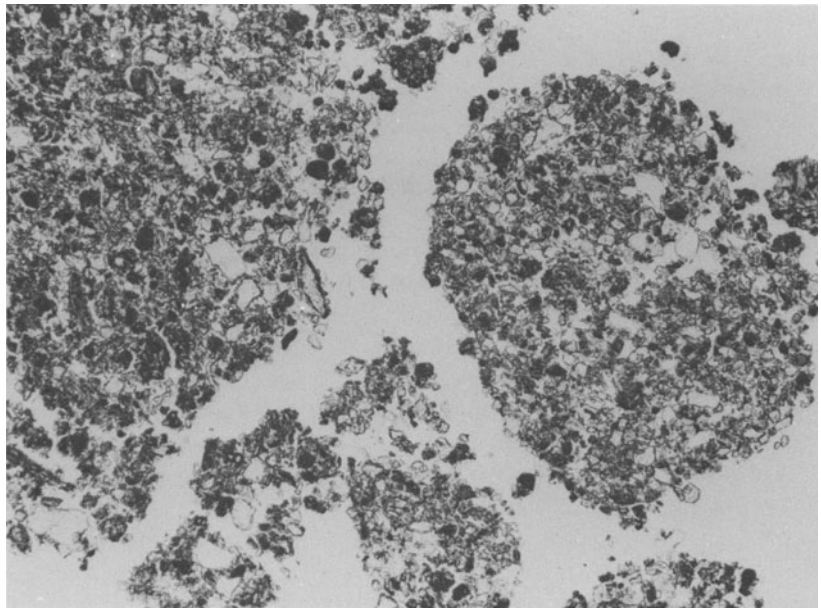

Figure 52. Mull-like rendzina moder, A_h horizon (see also Figures 26 and 53). Organic and mineral fine substance (calcite grains) are intimately mixed, but both are present in their own constituents that are readily distinguishable from each other; plant residues almost completely absent. Distinct formation of large aggregates. The great rounded aggregate to the right is a diplopod dropping. A_h (Vienna woods, Austria). Ground thin section (20 μm), bright field, natural size 1.5 mm.

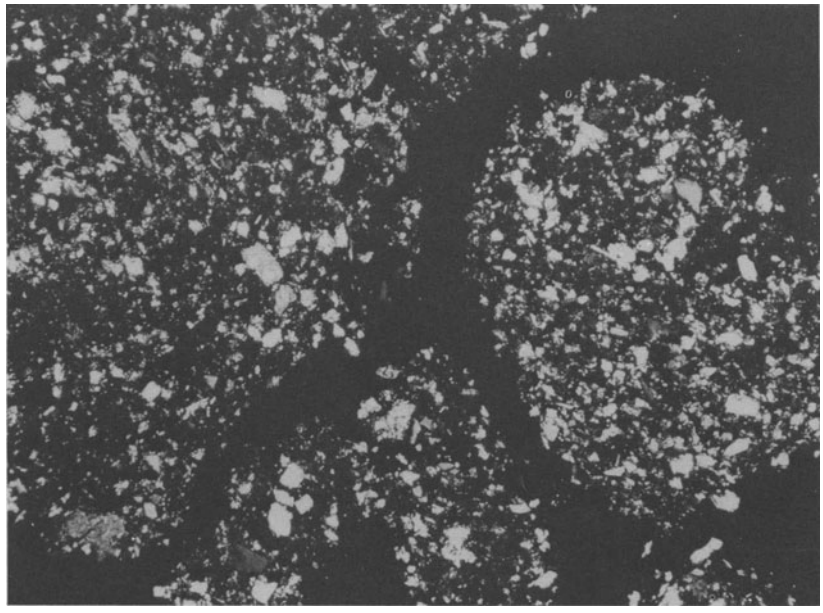

Figure 53. Like Figure 52, but under crossed polarizers. The calcite grains appear bright (fine sand and silt fraction, clay fraction missing).

5. *Mull*

Typical mull is characterized by a mineral humus horizon with a distinct clay content and a more or less pronounced crumb structure. It is colored brown or grey brown by organic matter. Apart from the color, the organic substance cannot be recognized macroscopically. It is more stable than in the humus forms discussed so far, through close attachment to the clay substance, namely forming of the clay humus complex (SCHEFFER and ULRICH [1960]). This humus form occurs in nutrient-rich soil formations with high biological activity. Mull formations under forest have sometimes a shallow decay layer under the litter; however, an holorganic humus substance layer is always absent.

The *decay layer* insofar as it is at present, resembles those of nutrient-rich moder formations. In addition to disintegrated plant residues, large amounts of droppings in manifold formations occur, especially large droppings of diplopods and the larger insect larvae. But signs of fungal degradative activities on the leaf residues are also found. Macroscopically, the most striking is a bleaching of the not yet disintegrated leaves, which is found frequently in forest soils. This, as the microscopic preparation shows, is a consequence of the disappearance of the leaf browning substances (for details, see Part III B 2 b).

In the *mineral humus horizon*, solitary intensely colored plant residues are sometimes found. Their amount varies with the season of the year; in late summer they have usually completely disappeared. They are often enveloped by mineral substances. Holorganic fine substance constituents are present only in exceptional cases. The main quantity of the organic substance exists as pigment of the mineral substance and is not recognizable as intrinsic particles, even at the highest microscopic magnifications (Figure 2).

The *fabric* of the mineral humus horizon is spongy fabric in the ecologically most favorable mull formations (Figure 2). If it is very loose at the surface of the mineral soil, the aggregates are hardly combined with each other and show their bulbous contours. Plant residues lie loosely between the aggregates. A spongy fabric occurs to usually no more than 5 cm depth. In the lower part of the A_h horizon, mostly a coherent fabric occurs, which is divided more or less by fissures (Figure 42). In ecologically less favorable mull formations this fabric extends to the surface of the mineral soil. Traces of activity of earthworms or enchytraeids also can be found in thin sections of such mull formations (see Parts IV A 3 and IV B 3).

The primary disintegration of the plant residues is due to the work of small arthropods, whose droppings are quickly consumed by earthworms. The earthworms, in addition, also attack soft plant residues directly. As they consume mineral substances with organic substances at the same time, the intimate blending leads to the formation of the clay-humus complex in the gut of the earthworms. Termites (GENNART *et al.* [1961], HARRIS [1955]), enchytraeids, and probably also julids (JONGERIUS [1961], DUNGER [1963]), as well as Diptera larvae act partly in a similar manner (see Part IV A 3).

The very small proportion of plant residues and the usually complete absence of holorganic fine substance particles indicate the intensity of the transformation in mull, which takes place here presumably because of the close admixture with the clay-rich mineral substance and terminates in the stable binding of the organic matter with clay. This is in complete contrast to the mineral humus horizon of raw humus, moder, and mull-like moder, where, as already mentioned, the organic constituents are not essentially different from those in the humus substance layer.

On the basis of micromorphological investigations, particularly of arable soils from bog and Anmoor, JONGERIUS [1961] and JONGERIUS and SCHELLING [1960] distinguish different varieties of mull. They name "protomull" a humus formation in which the organic and mineral parts are still incompletely mixed and numerous large and small plant residues may

still be recognized. This is at the same time the extreme example of a "heterogeneous mull." Classical mull, on the contrary, is an "homogeneous mull," in which the organic matter occurs only as pigment. "Postmull" is a form that exhibits breakdown of the crumb structure, decrease of the porosity, and brightening of the colors because of mineralization.

The subform occurring in the Tirs also shows low crumb stability and tendency to form cracks (KLINGE [1960]). The relationship of Tirs humus to Anmoor may also be recognized by the brownish-grey color shades in thin sections, and occasional occurrence of diatom shells and small, very dark to opaque pieces of tissue (KUBIENA [1957]). There are also cracks in the A_h horizon of most mull formations rich in clay. HOOVER and LUNT [1952] (further American literature quoted) list as macroscopically distinguishable mull subforms: firm mull, sand mull, coarse mull, medium mull. (A similar subclassification is also given by EHWALD [1956].) Fine mull, which has also been described by Hoover and Lunt, might in most cases turn out to be similar to mull-like moder on microscopic examination. On the other hand sand mull, in spite of very high sand content and low nutrient status, might often be a true mull formation which owes its origin largely to a favorable microclimate (VON ZEZSCHWITZ [1965]).

6. *Tangel*

Tangel (KUBIENA [1953, 1970]) is a complex humus form with features of raw humus and of mull or mull-like moder. The decay layer, however, shows a characteristic formation which makes it necessary to treat it as a distinct humus form. It is up to several decimeters thick and consists of slightly disintegrated plant residues in which mineral aggregates are intermingled (KUBIENA [1948], ZÖTTL [1965]). A holorganic humus substance layer is only present in oligotrophic or dystrophic forms (Figure 13). Tangel occurs mainly in high mountains and only under a vegetation that produces litter not easily decomposable (in the Alps, above all *Pinus mugo* and alpine dwarf bushes). The mineral soil must always show a certain clay or at least silt content.

The *decay layer* of tangel is also called tangel layer. It shows slightly to moderately disintegrated plant residues. The characteristic is the deposit of mineral aggregates, which contain numerous chewed plant residues (Figure 18). Formations on limestone, called tangel rendzinas contain, in the mineral aggregates, calcite fragments easily recognizable by polarization optics.

The decay layer does not pass abruptly but continuously into the *mineral humus horizon.* In particular, in its upper part, considerable quantities of fairly large plant residues are intimately mixed with the mineral material. Rather large amounts of only slightly changed fragments of root cortex are often noticeable, especially under *Pinus mugo* cover.

In mineral soil horizons more abundant in clay, the mineral aggregates in the decay layer and the whole mineral humus horizon have the same features as described for earthworm droppings and spongy fabric in the previous section (mull). In soils poorer in clay, in contrast, these parts show more of the features of mul-llike moder.

By the admixture of mineral material (especially if it contains much clay or lime) into the decay layer, acid humus substances, formed during the decomposition of the plant residues, cannot become active. Indeed, their effects (*e.g.*, dissolution of films of iron oxides from sand grains) can never be observed.

Dystrophic tangel shows a decay layer that resembles raw humus. But even here the mineral humus horizon is formed as mull-like moder or mull. In the case of shallow decay layers there are transitions to mull, which may occasionally be found at the mountain level.

VI. Methods

A short survey will be given here of the most important methods employed in work on

humus microscopy. The applicability of the methods to materials and problems will be indicated. Details of working techniques, however, are not presented here; refer to the literature quoted.

All the methods are derived originally from the fields of mineralogy, biology, and medicine, in which microscopic work has been done much longer than in soil science. The methods have been partially modified for use in humus research. In many cases, however, methodical procedures can be exactly the same as in the original fields of study. It is then simply a question of the application of mineralogical and histological methods to problems of humus research. Relatively few special methods of this kind have been adopted. For the future there are further significant possibilities. In the following, only those methods that have in fact already been used in humus microscopy are quoted.

Older techniques of micromorphological soil investigations, especially incident light and isolation techniques, are treated by KUBIENA [1938]. The soil thin section technique is presented by BREWER [1964]. A short review of humus micromorphological methods is given by BABEL [1971b]. For macromorphological and micromorphological techniques in humus research, see also BABEL [1972b]. For biological microtechnique JOHANSEN [1940] and ADAM and CZIHAK [1964] may be mentioned. An extensive older account of staining and detection reactions in botany is given by MOLISCH [1921]. A more recent, brief presentation of staining methods is that by BAKER [1958]. Optical procedures are to be found in books on microscopy, of which FREUND (volume I/1 [1957]), RINNE and BEREK [1953], and OSTER and POLLISTER [1955/56] (some parts newly revised) may be mentioned here. Further literature references are to be found in the books quoted here.

A. Preparatory Work

1. *Sampling in the Field*

If fabric analyses are intended, samples must be taken in their natural arrangement. For this purpose different appliances such as tin boxes or cylindrical augers are used (KUBIENA [1953], ALEXANDER and JACKSON [1955], BREWER [1964]). Recently sampling after freezing by liquid nitrogen or carbon dioxide ice has been proposed especially for loose humus layers (BLEVINS *et al.* [1968]) or for soil zoological investigations (ANDERSON and HEALY [1970]). For investigations of the decomposition of plant residues and of humus formation, separate bag samples of the individual subhorizons should be taken in the finest possible subdivision.

2. *Methods for the Isolation and Enrichment of Certain Components*

The normal and most straightforward method of fractionation is the mechanical isolation of the desired humus components. For this, the work can be done with dissecting needles and forceps under the stereomicroscope. KUBIENA [1938] has also used the micromanipulator for such purposes.

Enrichments of particular constituents may be obtained additionally in various indirect ways. Thus, KROLL and MEYER [1959] worked with grain size fractionations. SEKERA [1956] has obtained organic residues from mineral soil by means of a density fractionation. In pollen analysis the accumulation of pollen by chemical means is commonly used (*e.g.*, FAEGRI and IVERSEN [1964]).

Since a great number of special methods can be applied to the various morphologically differentiatable particles directly in the microscopic preparation of the whole sample, the isolation of the constituents can often also be disregarded.

3. *Production of Microscopic Preparations*

(a) Ground Thin Sections

Just as for investigations of mineral soil, the ground thin sections are used as standard preparations for morphological humus investigations. They are usually prepared from samples in natural arrangement.

To be able to produce thin sections of humus samples, the samples must be impregnated with a material that hardens completely. The same impregnating agents are used as for sections of mineral soils. Today, polyester synthetic resins are generally used (ALTEMÜLLER [1956b, 1962], BREWER [1964]). As these are not miscible with water, drying of the samples before impregnation is necessary. Some authors use the milder freeze-drying in place of the usual air-drying (ALEXANDER and JACKSON [1955], GADGIL [1963], STEPHAN [1969]). For the further preparation procedures—sawing up of the impregnated material, grinding, cementing to the microscope slide—reference should be made to BREWER [1964]. Recently several modifications and improvements of the embedding and preparation techniques have been published in the journals of soil science (*e.g.*, GILE [1967], GUERTIN and BOURBEAU [1971]).

Thin sections may be made from samples of all humus forms. Real difficulties do not thereby arise. However, some slight disturbances and artifacts may be sometimes produced. The following data are applicable to impregnation with the German synthetic resin, Vestopal H (ALTEMÜLLER [1962]). Occasionally the embedding agent is colored yellow by humus samples. Also, fluorescing substances can penetrate, in rare cases, from the sample into the synthetic resin. The polymerization of the synthetic resin can sometimes be somewhat delayed (ALTEMÜLLER and BANSE [1964]). Particularly with inadequately dried samples, strain birefringence can occur in the synthetic resin.

Parts that have not been impregnated may be lost during grinding. This happens sometimes with the interior of needle residues, if their epidermis and hypodermis are well preserved and prevent impregnation of the interior.

The morphology of the organic constituents is altered appreciably only in rare instances. The shrinkage by the previous drying can be considerable with strongly decomposed material. Shrinkage could be avoided by impregnation of wet samples. Methods of wet impregnation fully satisfactory for any kind of soil sample do not exist. They would be of special importance for fabric analysis of strongly decomposed material. Some experiments for wet impregnation of peat samples have been performed with carbowax 6000. This is an artificial resin miscible with water. Because of its softness (similar to talc), special cutting, grinding, and polishing techniques must be used (MACKENZIE and DAWSON [1961], LANGTON and LEE [1965]). Carbowax 6000 cannot be used for soil samples rich in sand. Preparation of those samples without too much shrinkage may be possible by dehydration in an alcohol series previous to the transfer to a polyester resin (LUND and BEALS [1965]). Shrinkage is diminished significantly by freeze-drying (measurements by MENGE [1965]). On the other hand, under higher magnification the structures of tissue residues occasionally seem somewhat swollen as compared with corresponding material in sliced thin sections. Very bright lobular margins around the organic constituents which sometimes occur especially in sections of wet moder formations, are likewise probably artifacts (Figure 51; Section V D 1 c).

Thin sections serve largely for the analysis of the aggregate and the elementary fabric (cf. Section II B). Furthermore, they provide a survey of the kind and proportions of the constituents. More detailed investigations of the constituents, in contrast, are performed more advantageously on sliced thin sections or debris preparations (see below).

Usually sections of 20 μm in thickness are suitable. Where mainly fabric analysis at low magnifications is involved, even 30 or 40 μm sections suffice. Very strongly colored material, on

the contrary, must be ground thinner so as to become transparent. With Vestopal H as the impregnating agent, sections of 6 to 8 μm thick may be easily produced. It is strongly recommended that in micromorphological publications the thickness of sections and the microscopic magnification used should be given, since many observed morphological properties, such as opacity or amorphousness, are dependent on these data.

(b) Thin Sections by Slicing Techniques

Sections can also be sliced from naturally arranged humus samples. A prerequisite of most methods is that the samples should be mineral-free.

Various substances which are used in biology or medicine have been tested as impregnating agents. *Cremolan* has proved to be very good in the preparation of peat sections (PUFFE and GROSSE-BRAUCKMANN [1963]). It also has the advantage of being miscible with water, so the peat samples need not be dried. Sections 10 μm thick are cut with the microtome.

Paraffin has been likewise used in making peat sections (RADFORTH and EYDT [1958]). *Agar-agar* was used by HAARLØV and WEIS-FOGH [1953, 1955] for the impregnation of organic layer samples. Before impregnation, fixing with formaldehyde vapor was carried out because mainly microbiological investigations were intended. In this method cutting is done with razor blades. Sand-containing samples also can be cut, but the sand grains are pushed out by the razor blade. In this way, only sections of several 100 μm thickness can be obtained. MINDERMAN [1956] has developed this method further in that, after impregnation, for which he uses *gelatine*, the sand is dissolved out of the impregnated material with hydrofluoric acid. Sectioning is likewise performed with razor blades; even from originally sand-containing samples, section thicknesses may be obtained down to 7·5 μm. Another improvement of the gelatine embedding technique to get large, but rather thick sections (1 mm) for studies of animal positions in the soil, has been proposed by ANDERSON and HEALY [1970].

The subsequent techniques of mounting and covering of the sections are the same as used in biology and medicine.

Sliced sections have several advantages over ground sections. Instead of single sections, series of immediately successive sections may be prepared, and this does not require appreciably more effort. For impregnation with cremolan, agar-agar, or gelatine, drying is not necessary, so that corresponding artifacts are avoided. For staining and other manipulations, sliced thin sections are more easily accessible than sectioning by grinding.

Sliced thin sections are prepared, in addition, for the microscopic investigation of isolated plant residues (BABEL [1964a]). In this case, in contrast to the preparation of fresh tissues, fixing can be omitted. Paraffin may usually serve as the embedding medium. With such thin sections (sliced) there is another advantage over ground sections: the ease with which desired orientations may be obtained.

(c) Debris Preparations

For the investigation of the fine substance debris preparations can be made (Figure 11; BABEL [1965a]). In this case one can use dry material, or suspensions. On the microscope slide the flat or elongated parts orient themselves in a manner advantageous for observation.

For direct investigation of the soil microflora, several other preparation methods, such as growth plates, are employed (see Section III C 2 c).

B. Microscopic Investigations

The object of the microscopic investigation of natural humus formations is the constituent analysis and the fabric analysis (Part II). For constituent analysis (Part III) ground thin sec-

tions, sliced thin sections, and debris preparations are used. The interpretation of constituents according to their histological origin is given prevailingly by comparing morphological investigations. The chemical information obtained in this way is supplemented by microscopic detection reactions. For fabric analysis (Part IV) ground thin sections are used prevailingly. Besides comparing morphology, quantitative microscopic methods play an important role in fabric analysis.

1. *Techniques of Qualitative Microscopic Investigation*

With the stereomicroscope, work can be done directly on the sample. This also gives the connecting link between the macroscopic and the microscopic investigations. Constituents, which are indistinct in ground sections, are often easily recognized in the three-dimensional image of the stereomicroscope.

The microscopic investigation of ground sections, sliced sections, and debris preparations is usually made in *transmitted light*; *incident-light* investigations are only rarely employed, perhaps for opaque constituents. *Dark-field* illumination can be of value in the recognition of colorless structures, as well as for the clearer perception of color differences in organic parts, which show varying degrees of humification. *Phase-contrast* illumination also helps to make visible colorless parts, as for example, hyaline fungal hyphae. For the determination of the light refraction of humus constituents, the phase-contrast method has been used only in preliminary studies (ALTEMÜLLER and BANSE [1964]).

The *polarizing microscope* is also employed for qualitative investigations. Colorless cell walls and colorless mineral grains become visible by their birefringence (for detection of cellulose by birefringence see Part VI B 3). Fabric analysis investigation at half-crossed polarizers are often used, whereby pores (grey) can be differentiated from mineral grains (darker or brighter). *Fluorescence illumination* is also of great importance. Nearly all cell walls show primary fluorescence, so that tissue structures can be seen more distinctly in the fluorescence microscope. Small cell wall residues, which often occur in the organic fine substance and in humus mineral horizons can be found by fluorescence; the fluorescence microscope gives much more distinct pictures of such objects than the polarizing microscope (BABEL [1969]). (For lignin detection by fluorescence microscope see Part VI B 3.) The *interference microscope* has not been used directly in humus micromorphology.

Electron microscopic investigations have still scarcely been applied to humus micromorphological problems (BEUTELSPACHER [1955a, b]). Electron microscopic studies in neighboring fields, for example, in wood protection, however, also offer direct humus micromorphological information (LIESE and SCHMID [1962]).

For morphological comparison, besides a collection of permanent microscopic preparations, *microphotographs* are a very important aid (HEUNERT [1959], MICHEL [1962]). Moreover, microphotographs can serve for the prosecution and documentation of optical and chemical investigations that are performed on the microscopic preparations. Color photographs are by far superior to black and white photographs in most cases. The object under investigation nearly always is strongly differentiated in color. The color is an important feature of the organic constituents. Only in investigations of the void fabric are black and white photographs fully satisfactory.

2. *Techniques of Quantitative Microscopic Investigation*

A book edited by KUBIENA [1967] comprises several papers on techniques of micromorphometric soil analysis. The works of KUBIENA, BECKMANN, and GEYGER [1967], JONGERIUS [1963], JONGERIUS and JAGER [1964], GEYGER [1967], and GEYGER and BECKMANN [1967]

contribute also to the application of such methods on problems of microscopic humus investigation.

Measurements of *length* and *thickness* as well as *countings* supplement the qualitative descriptions. The main subject of micromorphometric soil analysis are measurements of areas in the thin section. Under normal conditions they are measurements of *volumes* simultaneously. The most important method is point counting, which can be applied for many purposes, and requires but very simple equipment (NEUER [1966]). By point counting the volume ratio of pores and of any interesting groups of constituents or aggregates can be determined (*e.g.*, plant residues, organic fine substance, root residues, droppings). Structure photograms may be used for determination of volumes of pores and great mineral grains (KUBIENA, BECKMANN, and GEYGER [1962]). Also the *surfaces* of constituents and aggregates can be determined on structure photograms (GEYGER and BECKMANN [1967]). Measurements of *size of pores and particles* can be made by the particle size analyzer (Zeiss; *e.g.*, GEYGER and BECKMANN [1967]). Countings and measurements of sizes and volumes can now be made by the electronic quantimet-apparatus, when the groups of constitutents to be measured show enough difference in brightness (JONGERIUS [1969].

Estimation methods have proved to be of great value when the material under investigation consists of a great lot of samples. Such methods were developed in investigations applying humus micromorphology to ecological problems (BABEL [1967, 1972b]). Any micromorphological features which seem to be of interest can be estimated in scales from 0 to 5 according to their intensity or frequency. The estimation figures may be evaluated by simple statistical methods.

3. *Microscopic Detection Methods*

Optical and chemical methods so far applied to microscopic preparations of humus may serve to render cell and tissue structures visible. They may also give information about kind and degree of decomposition of the plant substances involved.

(a) Optical Methods

The positive *birefringence of cellulose* is one of the most important aids to microscopic humus investigations (principles in RUCH [1956], FREY-WYSSLING [1959]; first applications in humus investigation in GROSSKOPF [1935], KUBIENA [1943a]). Birefringent structures in plant residues indicate that cellulose is still present (*e.g.*, Figures 34, 27, 19). Naturally, it must be borne in mind that the brightening of cellulose residues under crossed polarizers can be almost completely masked by encrustations with strongly colored material. Especially in the mesophyll of leaves, very careful observations are necessary, since the cellulose walls are very thin. Besides the cellulosic cell walls, there are few birefringent organic constituents in humus. A smaller and negative birefringence may be often observed in the cuticular layer. It seems to be due to membrane waxes. The chitin walls of fungi usually do not show any distinct birefringence, but the chitin parts of soil animals are often strongly birefringent.

The synthetic resins of ground thin sections, when too rapidly polymerized, may show enough birefringence to impair observation of the birefringence of the organic parts.

The *autofluorescence* of many organic substances likewise has been used in humus microscopic investigations. A review on basics, techniques, and applications in humus micromorphology is given by BABEL [1972a]. For the application of fluorescence microscopy to biological objects, see PRICE and SCHWARTZ [1956]. In the field of coal petrography, fluorescence microscopic methods are also used (MALAN [1962], JACOB [1969]). MELHUISH [1968] determined living roots in polished blocks by their fluorescence. Single cell wall parts may often be detected in ground thin sections by fluorescence (Figures 24, 30). Sometimes they can be determined by their characteristic fluorescence colors. Thus, cuticulae usually fluoresce quite

strongly yellowish or bluish green, cell walls of the mesophyll weakly yellowish, lignified cell walls strongly light blue to greenish blue (Figure 4). After removal of the yellowish decomposition products by means of sodium hypochlorite, even the cell walls in the mesophyll often appear bluish. Colorless hyphae sometimes show whitish or bluish autofluorescence (Figure 28).

Autofluorescence can result from traces of accompanying substances in the fluorescing particle. The fluorescence of lignified cell walls, however, is due to lignin; therefore the degradation of lignin can be followed by means of the fluorescence. In the course of decomposition of lignified tissues, the blue fluorescence decreases (JABLONSKI [1963], ALTEMÜLLER and BANSE [1964], BABEL [1964a]). Likewise the autofluorescence of the other organic residues decreases in the course of decomposition (observations by the author). Strongly fluorescing decomposition neoformations, on the contrary, have been found only in two instances, which may well be considered as not yet fully established (JABLONSKI [1963], ALTEMÜLLER and BANSE [1964]). Leaf-browning substances sometimes show weak fluorescence (BABEL [1972a]).

The synthetic resins of the ground thin sections usually fluoresce very little so that the observations of the fluorescence of organic particles are not disturbed.

Secondary fluorescence, hence fluorescence after staining with fluorochromes, is used in the direct investigation of the soil microflora (see Section III C 2 c). In the secondary fluorescence of undecomposed and decomposed tissues, differences were found by PAULI [1958, 1960] which, however, were not very distinct in microscopic preparations.

Microspectrographic determinations of the ultraviolet absorption of humus constituents were instituted by the author in relation to the questions of lignin degradation (see Section III B 2 d β, for methods, see RUCH [1960]).

(b) Chemical Methods

As a rule these methods may be performed on sliced thin sections and on debris preparations. With ground thin sections, they are of only limited applicability, since the reagents penetrate only poorly into the synthetic resin used as impregnation agent. (It is practically impossible to dissolve the resin out of the preparation.) GAUTIER and HOLD [1960] give staining times of more than 24 hours for 1 μm thick sections of Vestopal W impregnations. With soil ground thin sections, however, some reactions may nevertheless be obtained in much shorter times (BABEL [1964c]). In 20 to 30 μm thick sections the organic parts were nearly completely decolorized in a 90-minute treatment with sodium hypochlorite. In a 5-minute treatment with yellow potassium ferrocyanide, the iron oxide-containing parts were colored blue and became thereby distinguishable from organic parts. The short times sufficed because here the reagents could attack particles that were in the surface of the thin sections (THOENES [1960]). In order to make microorganisms visible, especially bacteria, ALEXANDER and JACKSON [1955] as well as JONES and GRIFFITHS [1964] suggest staining the samples before impregnation with synthetic resin.

Various authors have carried out the usual *botanical detection reactions* for the most important cell wall substances in sliced thin sections, in particular, the methods for detection of lignin with phloroglucinol, of cellulose with chlorozinc iodide, and of cutin with Sudan III (HANDLEY [1954], HOLLING [1958], KONONOVA [1961], FRERCKS and PUFFE [1964], BABEL [1964a, 1964b]; for literature on the methods, see introduction to Section VI.). BABEL [1972b] has applied these reactions—in combination with optical methods—also to debris preparations of the fine substance. Indications of chemical changes in the decomposition of lignified cell walls may possibly be obtained also by staining with Ruthenium red and with Schiff's reagent (BABEL [1964a]).

Contrast stainings have likewise been performed on sliced soil sections (HANDLEY [1954], PUFFE and GROSSE-BRAUCKMANN [1963]). HAARLØV and WEIS-FOGH [1955] have stained living

cells or cells that had just died with Violamine in agar-agar sections. For humus microscopic investigations one should always leave control preparations unstained, as the natural colors are a very important morphological feature.

In the investigation of colored organic neoformations, *sodium hypochlorite* has proved useful in various respects. This reagent is frequently used in botanical microtechniques for clearing, and was applied by HANDLEY [1954] for the first time to humus microscopic work. The colored organic substances are distinguished characteristically by the rapidity of decolorization and the speed of solution in sodium hypochlorite. Above all, however, the colored organic parts are distinguished from the uncolored cell walls, because the former are quantitatively soluble but the latter insoluble. Thus, fresh lignified secondary walls are not dissolved, but their brown-colored residues are dissolved rather rapidly (BABEL [1964a]). For the purely morphological investigation, sodium hypochlorite is important as a clearing agent. It often can reveal tissue structures that had been masked by colored substances (BABEL [1964b]). With sodium hydroxide, certain solution effects on colored organic residues are likewise obtained, but the results are by no means so clear as with sodium hypochlorite (HANDLEY [1954], VON BUCH [1962]).

In the search for characteristic stainings for humus substances, *Safranine T* was used by HOLLING [1958]. This dyestuff, however, also stains undecomposed lignified cell walls. In fact, the best microscopic characteristics of humification products are their own yellow, brown, or red colors.

REFERENCES

Adam, H., and G. Czihak [1964]. *Arbeitsmethoden der makroskopischen und mikropischen Anatomie* Stuttgart: Fischer.

Alexander, F. E. S., and R. M. Jackson [1955]. Preparation of sections for study of soil microorganisms. In D. K. Mc. E. Kevan ed. [1955]. *Soil Zoology*. Proc. Univ. Nottingham, 2nd. Easter School Agri. Sci. London: Butterworth.

Allison, F. E. [1968]. Soil aggregation—some facts and fallacies as seen by a microbiologist. *Soil Sci.* 106: 136–143.

———, and C. J. Klein [1961]. Comparative rates of decomposition in soil of wood and bark particles of several softwood species. *Proc. Soil Sci. Soc. Am.* 25: 193–196.

———, and R. M. Murphy [1963]. Comparative rates of decomposition in soil of wood and bark particles of several species of pine. *Soil Sci.* 27: 309–312.

Altemüller, H. J. [1956]a. Mikroskopische Untersuchung einiger Löss-Bodentypen mit Hilfe von Dünnschliffen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 72: 152–167.

———. [1956b]. Neue Möglichkeiten zur Herstellung von Bodendünnschliffen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 72: 56–62.

———. [1960]. Mikromorphologische Untersuchungen an einigen Gipskeupebröden im Raum Iphofen. *Bayer. Landw. Jb.* 37:70–85.

———. [1962a]. Beitrag zur mikromorphologischen Differenzierung von durchschlämmter Parabraunerde, Podsol-Braunerde und Humus-Podsol. *Z. Pfl.-Ernähr. Düng Bodenk.* 98: 247–258.

———. [1962b]. Gedanken zum Aufbau des Bodens und seiner begrifflichen Erfassung. *Z. Kulturtechnik* 3: 323–336.

———. [1962c]. Verbesserung der Einbettungs- und Schleiftechnik bei der Herstellung von Bodendünnschliffen mit Vestopal. *Z. Pfl.-Ernähr. Düng. Bodenk.* 99: 164–177.

———. [1966]. Die morphologische Untersuchung des Bodengefüges. In *Handbuch der Pflanzenernährung und Düngung*, Band II/1, Wien, New York: Springer.

———. und H. J. Banse [1964]. Die Bedeutung der Mikromorphologie hinsichtlich der organischen

Düngung. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd. Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———. und H. Klinge [1964]. Mikromorphologische Untersuchungen über die Entwicklung von Podsolen im Amazonasbecken. In A. Jongerius, ed., [1964]. *Soil Micromorphology*. Proc. 2nd Inter. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———, and C. Tietjen [1967]. Some observations on animal activity in compost. In Graff and Satchell, *Progress in Soil Biology*. Proc. Coll. Dynamics Soil Communities, 1966. Vieweg: Braunschweig.

Anderson, J. M. [1970]. Observations on the vertical distribution of Oribatei [Acarina] in two woodland soils. 4. *Coll. Pedobiol.*, Dijon, 1970. Paris [1971]: I.N.R.A.

——, and J. N. Healey [1970]. Improvements in the gelatine-embedding technique for woodland soil and litter samples. *Pedobiol.* 10: 108–120.

Apinis, A. E. [1969]. Biocoenotic relationships of grassland soil fungi. *Mitt. flor.-soz. A. G., N.F., H.* 14: 68–85.

Aspiras, R. B., O. N. Allen, R. F. Harris, and G. Chesters [1971]. Aggregate stabilization by filamentous microorganisms. *Soil Sci.* 112: 282–284.

Babel, U. [1964a]. Dünnschnittuntersuchungen über den Abbau lignifizierter Gewebe im Boden. In A. Jongerius, ed. [1964]. *Soil Micromorphology*. Proc. 2nd Inter. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elseveir.

———. [1964b]. Opake organische Gemengteile in Auflagehumusformen. Scheffer-Festschrift 1964. Institut für Bodenkunde, Göttingen.

———. [1964c]. Chemische Reaktionen an Bodendünnschliffen. *Leitz-Mitteilungen* 3 (Nr. 1): 12–14.

———. [1965a]. Humuschemische Untersuchung eines Buchen-Rohhumus mittels mikrokopischer Methoden. *Mit. Ver. forst. Standortskunde* 15: 33–38.

———. [1965b]. Die Ansprache von Pflanzenresten im mikrokopischen Präparat von Humusbildungen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 109: 17–26.

———. [1967]. Vergleich von Mikrogefügemerkmalen einiger Humusbildungen mit Hilfe einer Schätzmethode. *Geoderma* 1: 347–357.

———. [1968/69]. Enchytraeen-Losungsgefüge in Löss. *Geoderma* 2: 57–63.

———. [1971a]. Gliederung und Beschreibung des Humusprofils in mitteleuropäschen Wäldern. *Geoderma* 5: 297–324.

———. [1971b]. Methods of investigating the micromorphology of humus. In H. Ellenberg, ed., *Integrated Experimental Ecology. Ecological Studies, Analysis and Synthesis*, Vol. 2, Berlin, Heidelberg, New York: Springer.

———. [1972a]. Fluoreszenzmikroskopie in der Humusmikromorphologie. Third Intern. Working Meeting on Soil Micromorphology, Wroclaw, Poland, Sept. 1969. Warszawa: Polska Akademia Nauk.

———. [1972b]. *Moderprofile in Wäldern—Morpholgie und Unsetzungsprozesse. Hohenheimer Arbeiten* 60, Stuttgart: Ulmer.

———. and R. Straub [1969]. Beziehungen makromorphologischer Merkmale von Humusprofileln zu der Behandlung und der Vegetation von Kahlschlagflächen. *Göottinger Bodenkundl. Ber.* 9: 125–169.

Bäbler, S. [1957]. Über die Verbräunung des Tabaks. Diss., Eidgenössische Technische Hochschule. Zürich: Juris-Verlag.

Baker, J. R. [1958]. *Principles of Biological Microtechnique*. London: Methuen, and New York: Wiley.

Bal, L. [1970]. Morphological investigation in two moder humus profiles and the role of the soil fauna in their genesis. *Geoderma* 4: 5–36.

———. [1973]. Micromorphological analysis of soils. Lower levels in the organization of organic soil materials. Thesis. University of Utrecht.

Barnett, H. L. [1958]. *Illustrated Genera of Imperfect Fungi*. Minneapolis: Burgess Publ.

Barratt, B. C. [1962]. Soil organic regime of costal sand dunes. *Nature* 196: 835–837.

———. [1964]. A classification of humus forms and micro-fabrics of temperate grasslands. *J. Soil Science* 15: 342–356.

———. [1965]. Decomposition of grass litters in three kinds of soil. *Plant Soil* 23: 265–269.

Barrett, B. C. [1967]. Differences in humus forms and their microfabrics induced by long-term top-dressings in hayfields. *Geoderma* 1: 209–227.

———. [1968a]. Micromorphological observations on the effect of land use differences on some New Zealand soils. *N.Z. J. Agric. Res.* 11: 101–130.

———. [1968b]. Macro- and micromorphological changes in topsoils under intensified grassland management. Ninth Intern. Congr. Soil Sci., Adelaide, Austr., Vol. 3, 211–219.

———. [1968/69]. A revised classification and nomenclature of microscopic soil materials with particular reference to organic components. *Geoderma* 2: 257–271.

Bartholomew, W. V. [1963]. The role of microorganisms in the formation and decomposition of organic compounds in soil. In R. A. Silow: The use of isotopes in soil organic matter studies. Rep. FAD/IAEA Techn. Meeting, Brunswick-Völkenrode, Sept. 1963.

Bavendamm. W. [1951]. "Mikroskopisches Erkennen und Bestimmen von holzbewohnenden und holzzersetzenden Pilzen." In H. Freund, ed. *Handbuch der Mikroskopie in der Technik* 5/2.

Beckmann, W., and E. Geyger [1967]. Entwurf einer Ordnung der natürlichen Hohlraum-, Aggregat- und Strukturformen im Boden. In W. Kubiena: *Die Mikromorphometrische Bodenanalyse.* Stuttgart: Enke.

Benecke, P., and U. Babel [1969]. Untersuchungen über die Auswirkung des Fichten-Reinanbaus auf Parabraunerden und Pseudogleyen des Neckarlandes. 3. Humusmorphologie und Bodengefüge. *Mitt. Ver. Forstl. Standortskunde* 19: 81–89.

Beutelspacher, H. [1955a]. Wechselwirkung zwischen anorganischen und organischen Kolloiden des Bodens. *Z. Pfl-Ernähr. Düng. Bodenk.* 69: 108–115.

Beutelspacher, H. [1955b]. Natürliche Fadenkolloide und Krümelbildung. *Landbauforschung Völkenrode* 5 (Nr. 4): 90–92.

Biwer, A. [1961]. Quantitative Untersuchungen über die Bedeutung der Asseln und der Bakterien für die Fallaubzersetzung unter Berücksichtigung der Wirkung künstlicher Düngemittelzusätze. I und II. *Z. Angewandte Entomologie* 48: 307–328, 377–394.

Blevins, R. L., G. M. Aubertin, and N. Holowaychuk [1968]. A technique obtaining undisturbed soil samples by freezing in situ. *Soil Sci. Soc. Am. Proc.* 32: 741–742.

———, N. Holowaychuk, and L. P. Wilding [1970]. Micromorphology of soil fabric at tree root-soil interface. *Proc. Soil Sci. Soc. Am.* 34: 460–465.

Blume, H. P. [1965]. Die Charakterisierung von Humuskörpern durch Streu und Humusstoffgruppen-analyse unter Berücksichtigung ihrer morphologischen Eigenschaften. *Z. Pfl.-Ernähr. Düng. Bodenk.* 111: 95–113.

Bottner, P. [1970]. La matière organique des principaux types de sols sous l'étage bioclimatique du chêne vert dans le midi de la France. *Sci Sol* No. 1: 3–18.

Brauns, F. E., and D. A. Brauns [1960]. *Chemistry of Lignin.* Suppl. vol. New York and London: Academic Press.

Bremner, J. M. [1955]. Recent work on soil organic matter at Rothamsted. *Z. Pfl.-Ernähr. Düng. Bodenk.* 69: 32–38.

Brewer, R. [1964]. *Fabric and Mineral Analysis of Soils.* New York and London: Wiley.

———, and J. R. Sleeman [1963]. Pedotubules: their definition, classification and interpretation. *J. Soil Sci.* 14: 156–166.

von Buch, M. [1962]. Vergleichende chemische und mikromorphologische Untersuchungen bei der Extrahierung von Huminstoffen aus Waldböden. *Z. Pfl.-Ernähr. Düng. Bodenk.* 97: 255–265.

Burgeff, H. [1961]. *Mikrobiolgie des Hochmoors.* Stuttgart: Fischer.

Burges, A. [1963]. The microbiology of a podzol profile. In Doeksen and van der Drift, eds., *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek, Amsterdam: North Holand Publishing Company.

———. [1967]. The decomposition of organic matter in the soil. In Burges and Raw, eds, *Soil Biology.* London, New York: Academic Press.

———, and F. Raw, eds. [1967]. *Soil Biology.* London, New York: Academic Press.

Butin, H. [1961]. Versuche zum künstlichen Verblauen von Kiefernsplintholz mit dem Pilz Pullularia pullulans [de Bary] *Berkh. Angewandte Botanik* 35: 94–106.

Cholodny, N. [1930]. Über eine neue Methode zur Untersuchung der Bodenmikroflora. *Archiv Mikrobiologie* 1.

Coulson, C. B., R. J. Davies, and D. A. Lewis [1960a, b]. Polyphenols in plant, humus and soil. I. Polyphenols of leaves, litter, and superficial humus from mull and mor sites. II. Reduction and transport by polyphenols of iron in model soil columns. *J. Soil Sci.* 11: 20–29, 30–44.

Dahlman, R. C. [1968]. Root production and turnover of carbon in the root-soil matrix of a grassland ecosystem. In USSR Academy of Sciences, Intern. Symp. USSR 1968. Leningrad: Nauka.

———, and C. L. Kucera [1965]. Root productivity and turnover in native prairie. *Ecology* 46: 84–89.

Davies, R. J. [1971]. Relation of polyphenols to decomposition of organic matter and to pedogenetic processes. *Soil Sci.* 111: 80–85.

———, C. B. Coulson, and D. A. Lewis [1964 a, b]. Polyphenols in plant, humus and soil. III. Stabilization of gelatin by polyphenol tanning. IV. Factors leading to increase in biosynthesis of polyphenols in leaves and their relationship to mull and mor formation. *J. Soil Sci.* 15: 229–309, 310–318.

Delecour, F., and G. Manil [1962]. Mikromorphologischer Beitrag zur Kenntnis der sauren Braunerden der belgischen Ardennen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 98: 219–224.

Deuel, H. [1960]. Interactions between inorganic and organic soil constituents. Trans. 7th Intern. Congr. Soil Sci., Madison, Wisconsin, Vol. 1, p. 38–53.

Devigne, J., and C. Jeuniaux [1961]. Origine tissulaire des enzymes chitinolytiques intestinaux des lombrics. *Arch. Intern. Physiol.* 69: 223–234.

Dimbleby, G. W. [1961]. Soil pollen analysis. *J. Soil Sci.* 12: 1–11.

Doeksen, J., and J. van der Drift, eds. [1963]. *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

Dommergues, Y., and F. Mangenot [1970]. *Ecologie microbienne du sol.* Paris: Masson.

van der Drift, J. [1964]. Soil fauna and soil profile in some inland-dune habitats. In A. Jongerius, *Soil Micromorphology.* Proc. 2nd Inter. Working Meeting on Soil Micromorphology Arnhem. Amsterdam: Elsevier.

———, and M. Witkamp [1960]. The significance of the breakdown of oak litter by Enoicyla pusilla Burm. *Arch. Néerl. Zool.* 13: 486–492.

Drozdova, T. V. [1959]. Chitin and its transformations in natural processes. Formation of melanoidins. *Usp. Sovrem. Biol.* 47: 277–296.

Dudas, M. J., and S. Pawluk [1969/70a]. Naturally occurring organo-clay complexes of orthic black chernozems. *Geoderma* 3: 5–17.

———. [1969/70b]. Chernozem Soils of the Alberta Parklands. *Geod.* 3: 19–36.

Dunger, W. [1956]. Untersuchungen über die Laubstreuzersetzung durch Collembolen. *Zoologisches Jahrbuch, Abt. Systematik, Ökologie und Geographie* 84: 75–98.

———. [1958]. Uber die Veränderung des Fallaubs im Darm von Bodentieren. *Z. Pfl.-Ernähr. Düng. Bodenk.* 82: 174–193.

———. [1963]. Leistungsspezifität bei Streuzersetzern. In Doeksen and van der Drift, eds., *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

———. [1964]. *Tiere im Boden.* Wittenberg: Ziemsen.

Edwards, C. A., and G. W. Heath [1963]. The role of soil animals in breakdown of leaf material. In Doeksen and van der Drift, eds. *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

Ehwald, E. [1956]. Über einige Probleme der forstlichen Humusforschung, insbesondere die Entstehung und die Einteilung der Waldhumusformen. Sitzungsberichte der deutschen Akademie der Landwirtschaftswissenschaften zu Berlin 5, (Nr. 12). Leipzig: Hirzel.

Erdtman, G. [1971]. Notes on the resistance and stratification of the exine. In J. Brooks *et al.*, *Sporopollenin* Proc. Symp. Geol. Dept., Imperial College, London. London, New York: Academic Press.

Esau, K. [1953]. *Plant Anatomy.* New York: Wiley, and London: Chapman and Hall.

Evans, D. D., and S. W. Buol [1968]. Micromorphological study of soil crusts. *Soil Sci. Soc. Am. Proc.* 32: 19–22.

Faegri, K., and J. Iversen [1964]. *Textbook of Pollen Analysis.* 2nd rev. ed. Oxford: Blackwell.

Falck, R. [1930]. Nachweise der Humusbildung und Humifizierung durch bestimmte Arten höherer Fadenpilze im Waldboden. *Forstarchiv* 6: 366–377.

Firbas, F. [1949]. Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen. 1. Band, Jena: Fischer.

———, and F. Broihan [1937]. Das Alter der Trockentorfschichten im Hils. *Planta* 26: 291–302.

Flaig, W., J. C. Salfeld, and K. Haider [1963]. Zwischenstufen bei der Bildung von natürlichen Huminsäuren und synthetischen Vergleichssubstanzen. *Landwirtschaftliche Forschung* 16: 85–96.

Franz, H., and L. Leitenberger [1948]. Biologisch-chemische Untersuchungen über Humusbildung durch Bodentiere. *Österr. Zool. Z.* 1: 498–518.

Frercks, W., and D. Puffe [1964]. Chemische und mikromorphologische Untersuchungen über den Zersetzungsgrad auf entwässertem und verschieden hoch aufgekalktem Hochmoor unter Grünland sowie in unkultiviertem, vorentwässertem Hochmoor. *Z. Kulturtechnik Flurbereinigung* 5: 149–171.

Freund, H. [1951]. *Handbuch der Mikroskopie in der Technik.* 8 Bände, Umschau-Verlag, Frankfurt/Main. Band I: Die optischen Grundlagen, Instrumente und Nebenapparate, Teil 1 [1957]: Allgemeines Instrumentarium der Durchlichtmikroskopie.

Frey-Wyssling, A. [1959]. *Die pflanzliche Zellwand.* Berlin, Göttingen, Heidelberg: Springer.

Führer, E. [1961]. Der Einfluss von Pflanzenwurzeln auf die Verteilung der Kleinarthropoden im Boden, untersucht an Pseudotritia ardua (Oribatei]. *Pedobiologia* 1: 99–112.

Gadd, O. [1957]. Wood decay resulting from rot fungi. *Papper och trä* 8: 363–374.

Gadgil, P. D. [1963]. Soil sections of grassland. In Doeksen and van der Drift, eds., *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

———. [1965]. Distribution of fungi on living roots of certain gramineae and the effect of root decomposition on soil structure. *Plant Soil* 22: 239–259.

Gäumann, E. [1951]. *Pflanzliche Infektionslehre.* 2. Aufl. Basel: Birkhäuser.

Gautier, A., and C. Hold [1960]. Technique de coloration histologique de tissus inclus dans des polyesters. *Experientia* 16: 124.

Gebhardt, H. [1971]. Zur Tonmineralzusammensetzung und Ton-Humus-Bindung in der Sequenz Schwarzerde-Parabraunerde (Griserde) der Hildesheimer Börde. *Göttinger Bodenkundl. Ber.* 19: 183–190.

Gennart, M., M. Kurbanovik, A. Nanson, and G. Manil [1961]. Contribution micromorphologique à l'étude de la biodynamique des sols forestiers équatoriaux. *Pedologie* 11: 110–122.

Geyger, E. [1967]. Die Strukturbildungen in den Humushorizonten von Böden der hohen Sierra Nevada, Spanien. *Geoderma* 1: 229–247.

———, and W. Beckmann [1967]. Untersuchungen zur Struktur eines Braunlehms unter montanem, immergrünem Regenwald in Peru. *Zeiss-Mitt.* 4: 185–207.

Ghitulescu, N., and G. Stoops [1970]. Étude micromorphologique de l'activité biologique dans quelques sols de la Dobroudja (Roumanie), *Pedologie* 20: 339–356.

van Gijzel, P. [1961]. Autofluorescence and age of some fossil pollen and spores. Proceedings K. Nederlandse akademie van wetenschappen Amsterdam Sect. B 64 (Nr. 1): 56–63.

———. [1971]. Review of the UV-fluorescence of fresh and fossil exines and exosporia. In J. Brooks et al. Proc. Symp. Geol. Dept., Imperial College, London. London, New York: Academic Press.

Gile, L. H. [1967]. A simplified method for preparation of soil thin sections. *Proc. Soil Sci. Soc. Am.* 31: 570–572.

Glathe, H. [1955]. Die direkte mikroskopische Untersuchung des Bodens. *Z. Pfl.-Ernähr. Düng. Bodenk.* 69: 172–176.

Goethe, J. W. [1807]. *Einleitung zur "Metamorphose der Pflanzen."* Jena.

Grabbe, K., and K. Haider [1971]. Die Huminstoffbildung und die Stickstoffverteilung bei der Strohrotte in Beziehung zur mikrobiellen Phenolbildung. *Z. Pfl.-ern. u. Bodenkunde* 129: 202–216.

Gračanin, Z. [1962]. Zur Genese, Morphologie und Mikromorphologie der Hangtorfbildung auf Kalksteinen in Kroatien. *Z. Pfl.-Ernähr. Düng. Bodenk.* 98: 264–272.

Graff, O. [1955]. Kleintiere bei der Strohrotte im Ackerboden. *Landbauforschung Völkenrode* 5: 81–83.

Graff, O., and J. E. Satchell, eds. [1967]. *Progress in Soil Biology.* Proc. Coll. Dynamics Soil Communities, 1966. Braunschweig: Vieweg.

Gray, T. R. G. [1967]. Stereoscan electron microscopy of soil microorganisms. *Science* 155: 1668–1670.

———, and T. F. Bell [1963]. The decomposition of chitin in an acid soil. In Doeksen and van der Drift, eds. *Soil Organisms.* Proc. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

———, P. Baxby, J. R. Hill, and M. Goodfellow [1967]. Direct observation of bacteria in soil. In Gray and Parkinson. *The ecology of soil bacteria.* Liverpool Univ. Press.

Grosse-Brauckmann, G. [1961]. Zur Terminologie organogener Sedimente. *Geologisches Jahrbuch* 79: 117–144.

———. [1963]. Zur Artenzusammensetzung von Torfen. (Einige Befunde und Überlegungen zur Frage der Zersetzlichkeit und Erhaltungsfähigkeit von Pflanzenresten.) *Berichte der Deutschen Botanischen Gesellschaft* 76: 22–37.

———. [1964.] Einige wenig beachtete Pflanzenreste in nordwestdeutschen Torfen und die Art ihres Vorkommes. *Geologisches Jahrbuch* 81: 621–644.

———, and D. Puffe [1964]. Untersuchungen an Torf-Dünnschnitten aus einem Moorprofil vom Teufelsmoor bei Bremen. In A. Jongerius, ed. *Soil Micromorphology.* Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem, Amsterdam: Elsevier.

Grosskopf., W. [1935]. Stoffliche und morphologische Untersuchungen forstlich ungünstiger Humusformen. *Tharandter Forstliches Jahrbuch* 86: 48–111.

Guertin, R. K., and G. A. Bourbeau [1971]. Dry grinding of soil thin sections. *Can. J. Soil Sci.* 51: 243–248.

Haarløv, N. [1955]. Vertical distribution of mites and collembola in relation to soil structure. In D. K. McE. Kevan, ed. *Soil Zoology*, Proc. Univ. Nottingham, 2nd Easter School Agric. Sci. London: Butterworths.

———, and T. Weis-Fogh [1953]. A microscopical technique for studying the undisturbed texture of soils. Oikos 4, 44–57. See also in D. K. McE. Kevan ed. *Soil Zoology.* Proc. Univ. Nottingham, 2nd Easter School Agric Sci. London: Butterworths.

Haider, K. [1965]. Untersuchungen über den mikrobiellen Abbau von Lignin. *Zbl. Bakteriol. I,* 198: 308–316.

———, and K. H. Domsch [1969]. Abbau und Umtsezungen von lignifiziertem Pflanzenmaterial durch mikroskopische Bodenpilze. *Archiv Mikrobiol.* 64: 338–348.

———, and J. P. Martin [1970]. Humic acid-type phenolic polymers from Aspergillus Sydowi culture medium. *Soil Biol. Biochem.* 2: 145–156.

———, and C. Schetters [1967]. Mesophile ligninabbauende Pilze in Ackerböden und ihr Einfluss auf die Bildung von Humusstoffen. In Graff and Satchell, eds. *Progress in Soil Biology.* Proc. Coll. Dynamics Soil Communities, 1966. Braunschweig: Vieweg.

———, S. Lim, and W. Flaig [1964]. Experimente und Theorien über den Ligninabbau bei der Weissfäule des Holzes und bei der Verrottung pflanzlicher Substanz im Boden. *Holzforschung* 18: 81–88.

Handley, W. R. C. [1954]. Mull and mor formation in relation to forest soils. Forestry Commission, Bulletin 23.

———, [1961]. Further evidence for the importance of residual leaf protein complexes in litter decomposition and the supply of nitrogen for plant growth. *Plant Soil* 15: 37–73.

Harris, W. V. [1955]. Termites and the soil. In D. K. Mc. E. Kevan ed. *Soil Zoology.* Proc. Univ. Nottingham, 2nd Easter School Agric. Sci. London: Butterworths.

Hartmann, F. [1952]. *Forstökologie.* Wien: Fromme.

———. [1965]. *Waldhumusdiagnose.* Wien: Springer.

Healey, J. N., and Russel-Smith, A. [1970]. Abundance and feeding preferences of fly larvae in two woodland soils. *Fourth Coll. Pedobiol.*, Dijon 1970. Paris [1971]: I.N.R.A.

Heinen, W., and H. de Vries [1966]. Stages during the breakdown of plant cutin by soil microorganisms. *Arch. Microbiol.* 54: 331–338.

Hennig, A. [1958]. Kritische Betrachtungen zur Volumen- und Oberflächenmessung in der Mikroskopie. *Zeiss-Werkzeitschrift* 30: 78–86.

Hensen, V. [1882]. Über die Fruchtbarkeit des Erdbodens in ihrer Abhängigkeit von den Leistungen der in der Erdrinde lebenden Würmer. *Landwirtsch. Jahrbuch* 11: 661–698.

Hess, C. [1965]. Über die Natur der Bindung des Humus in Schwarzerden und schwarzerdeartigen Böden, besonders in den Tirsen Marokkos. Diss., Göttingen.

Hesselmann, H. [1926]. Studier över barrskogens humustäcke. *Meddel. Stat. Skogsförsöksanst.* 22: 169–552.

Heunert, H. H. [1959]. *Praxis der Mikrophotographie.* 2. Aufl. Berlin, Göttingen, Heidelberg: Springer.

Hofmann, E. [1934]. *Paläohistologie der Pflanze.* Wien: Springer.

Holdheide, W. [1941]. Über zwei Funde prähistorischer Holzkohlen. *Ber. Deutschen Botanischen Gesellschaft* 59: 85–98.

Holling, R. [1958]. Untersuchungen zur Feinmorphologie und zum Chemismus einiger Torfe. Diss., Kiel.

———, and F. Overbeck [1961]. Über die Grösse der Stoffverluste bei der Genese von Sphagnumtorfen. *Flora* 150: 191–208.

Hoover, M. D., and H. A. Lunt [1952]. A key for the classification of forest humus types. *Proc. Soil Sci. Soc. Am.* 16: 368–370.

Huber, B. [1961]. *Grundzüge der Pflanzenanatomie.* Berlin, Göttingen, Heidelberg: Springer.

Hurst, H. M., and G. H. Wagner [1969]. Decomposition of ^{14}C-labelled cell wall and cytoplasmic fractions from hyaline and melanic fungi. *Soil Sci. Soc. Am. Proc.* 33: 707–711.

Jablonski, B. [1963]. The application of microscopical soil sections to investigations on the decomposition of plant residues in the soil. *Roczniki gleboznawcze* 13: 35–50.

———, and M. Radomska [1965]. The influence of different vegetable remainders upon the porosity of soil. Part I: Formation of soil pores under the influence of vegetable remainders. *Zeszyty Naukowe Wyzszej Szkoly Rolniczej we Wroclawiu, Rolnictwo* 19, Nr. 60.

Jacob, H. [1969]. Luminiszenz-Mikroskopie der organopetrographischen Bestandteile von Sedimentgesteinen. *Leitz-Mitt.* IV/8: 250–254.

Jakab, T., P. Dubach, N. C. Mehta, and H. Deuel [1962]. Abbau von Huminstoffen. I. Hydrolyse mit Wasser und Mineralsäuren. *Z. Pfl.-Ernähr. Düng. Bodenk.* 96: 213–217.

Jeanson, C. [1964]. Micromorphologie et pédozoologie expérimentale: Contribution à l'étude sur plaques minces de grandes dimensions d'un sol artificiel structuré par des Lombricides. In A. Jongerius, ed. *Soil Micromorphology.* Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———, [1970]. Structure d'une galérie de lombric à la microsonde électronique. IV. *Coll. Pedobiol.*, Dijon. Paris [1971]: I.N.R.A.

———, [1971]. Nouvelles données microscopiques sur la contribution de la faune à l'élaboration de la structure du sol. *C. R. Acad. Sci. Paris*, 272: 422–424.

Jenny, H., and K. Grossenbacher [1963]. Root soil boundary zones as seen in the electron microscope. *Proc. Soil Sci. Soc. Am.* 27: 273–277.

Johansen, D. A. [1940]. *Plant Microtechnique.* New York: McGraw-Hill.

Jones, D., and E. Griffiths [1964]. The use of thin soil sections for the study of soil microorganisms. *Plant Soil* 20: 232–240.

Jongerius, A. [1961]. De Micromorphologie van de Organische Stof. In Bodemkunde, voordrachten, gehouden op de B-cursus "Bodemkunde," September 1959. s-Gravenhage.

———. [1963]. Optic-volumetric measurements on some humus forms. In Doecksen and van der Drift, eds. *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships Oosterbeek. Amsterdam: North Holland Publishing Company.

———, editor [1964]. *Soil Micromorphology.* Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———. [1969]. Application of quantimet-apparatus in soil micromorphometry. Third Intern. Working Meeting Soil Micromorphology Wroclaw, Poland, Sept. 1969. Warsaw [1972]: Polska Akademia Nauk.

———. [1970]. Some morphological aspects of regrouping phenomena in Dutch soils. *Geoderma.* 4: 311–331.

Jongerius, A., and A. Jager [1964]. The morphology of humic gley soils (orthic haplaquolls) under different land use. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———, and L. Pons [1962a]. Soil genesis in organic soils. *Boor en Spaade* 12: 156–168.

———. [1962b]. Einige mikromorphologische Bemerkungen über den Vererdungsvorgang im niederländischen Moor. *Z. Pfl.-Ernähr. Düng. Bodenk.* 97: 243–255.

———, and J. Schelling [1960]. Micromorphology of organic matter formed under the influence of soil organisms, especially soil fauna. Seventh Intern. Congress Soil Sci., Madison, Wisconsin, Vol. 2.

Karpatschewski, L. O. [1960]. Micromorphological investigation of leaching and podzolization of soils in a forest. *Pochvovedenie* 1960 5: 43–52.

Kaunat, H., and K. Bernard [1969]. Pektinhydrolyse durch rhizosphärenspezifische Bakterien und Actinomyceten. Zentralbl. Bakt. etc. II, 123: 464–466.

Kevan, D. K. Mc. E., ed. [1955]. *Soil Zoology*. Proc. Univ. Nottingham, 2nd Easter School Agric. Sci. London: Butterworths.

Kickuth, R., B. Meyer, and H. Schonlau [1969]. Die divergierende Humus-Metabolik benachbarter Sauer-Braunerden und Rendzinen unter Wald im Licht organischer Stoffgruppenuntersuchungen. *Göttinger Bodenkundl. Ber.* 8: 1–61.

von Kirchner, O., E. Loew, and C. Schröter [from 1908]. *Lebensgeschichte der Blutenpflanzen Mittleuropas*. Stuttgart: Ulmer.

Klinge, H. [1960]. Beiträge zur Kenntnis tropischer Böden. 1. Die schwarzerdeartigen Böden auf der Oberen Serie der Schichten von San Salvador, El Salvador, Zentralamerika. *Z. Pfl.-Ernähr. Düng. Bodenk.* 89: 102–114.

Kononova, M. M. [1943]. Use of microscopical method for study of the origin of humic substances. *Pochvovedenie* 1943, 6–7.

———. [1961]. *Soil Organic Matter*. New York, Oxford, London, Paris: Pergamon Press.

Kowalinski, S. [1964a]. Moorsh soils and their metamorphoses effected by plough tillage. *Travaux de la Société des Sciences et des Lettres de Wroclaw Seria B*, Nr. 124.

———. [1964b]. Micromorphological properties of "moorsh" soils. In A. Jongerius, ed. [1964]. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem, Amsterdam, Elsevier.

———. [1969/70]. Interdependence between micromorphological and chemical properties in some zonal soils of the Karkonosze Mountains. *Geoderma* 3: 89–115.

———. and A. Kollender-Szych [1969]. Micromorphological and physicochemical examination of the decomposition degree of organic matter in some peaty muck soils. Third Intern. Working Meeting Soil Micromorphology, Wroclaw, Poland, Sept. 1969. Warszawa [1972]: Polska Akademia Nauk.

Kox, E. [1954]. Der durch Pilze und aerobe Bakterien veranlasste Pectin- und Cellulose-Abbau im Hochmoor unter besonderer Berücksichtigung des Sphagnum-Abbaus. *Archiv für Mikrobiologie* 20: 111–140.

Krause, W. [1964]. Zur Technik der mikromorphologischen Untersuchung nicht getrockneter Unterwasserböden. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem, Amsterdam: Elsevier.

Kroll, W., and B. Meyer [1959]. Die Charakterisierung von Humusformen durch Siebanalyse und mikromorphologische Untersuchung am Beispel einer Bodenserie auf mittlerem Buntsandstein bei Göttingen. *Landw. Forschung* 12: 12–17.

Kubiena, W. [1932]. Über Fruchtkörperbildung und engere Standortwahl von Pilzen in Bodenhohlräumen. *Archiv für Mikrobiologie* 3: 507–542.

———. [1935]. Über das Elementargefüge des Bodens. *Bodenkundliche Forschungen* 4: 380–412.

———. [1938]. *Micropedology*. Ames, Iowa: Collegiate Press.

———. [1943a]. Die mikroskopische Humusuntersuchung. *Z. Weltforstwirtschaft* 10: 387–410.

———. [1943b]. Beiträge zur Bodenentwicklungslehre. Entwicklung und Systematik der Rendsinen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 29: 108–119.

———. [1944]. *Suelo y formacion del suelo desde el punto de vista biologico*. Publ. del Inst. Español de Edafologia, Ecologia y Fisiologia Vegetal.

Kubiena, W. [1948]. [1948]. *Entwicklungslehre des Bodens.* Wien: Springer.
———. [1953]. *Bestimmungsbuch und Systematik der Boden Europas.* Stuttgart: Enke.
———. [1955a]. Die Bedeutung des Begriffes Humusform für die Bodenkunde und Humusforschung. *Z. Pfl.-Ernähr. Düng. Bodenk.* 69: 3–7.
———. [1955b]. Animal activity in soils as a decisive factor in establishment of humus form. In D. K. Mc. E. Kevan, ed. [1955]. *Soil Zoology.* Proc. Univ. Nottingham, 2nd Easter School Agric. Sci. London: Butterworths.
———. [1956]. Zur Mikromorphologie, Systematik und Entwicklung der rezenten und fossilen Lössböden. *Eiszeitalter und Gegenwart* 7: 102–112.
———. [1957]. Neue Beiträge zur Kenntnis des planetarsichen und hypsometrischen Formenwandels der Böden Afrikas. *Stuttgarter Geographische Studien* 69: 51–64.
———. [1967]. *Die mikromorphometrische Bodenanayse.* Stuttgart: Enke.
———. [1972]. New advances and applications of soil micromorphology. Third. Int. Working Meeting Soil Micromorphology, Wroclaw, Poland, Sept. 1969. Warszawa: Polska Academia Nauk.
———. [1970]. *Micromorphological features of soil geography.* N. Brunswick, N. J.: Rutger's Univ. Press.
———, W. Beckmann, and E. Geyger [1962]. Zur Untersuchung der Feinstruktur von Bodenaggregaten mit Hilfe von Strukturphotogrammen. *Zeiss-Mitteilungen* 2: 256–273.
Kühnelt, W. [1957]. Die Tierwelt der Landböden in ökologischer Betrachtung. *Verhand. Deutschen Zool. Ges. Graz,* 39–103.
———. [1958]. Zoogene Krümelbildung in ungestörten Böden. *Deutsche Akad. der Landw. wissenschaften Berlin, Tagungsberichte* 13: 193–199.
———. [1961]. *Soil Biology.* London: Faber.
———. [1963]. Über den Einfluss des Myzels von Clitocybe infundibuliformis auf die Streufauna. In Doeksen and van der Drift, eds. *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.
Küster, E., and K. Haider [1961]. Untersuchungen über die Farbstoffbildung bei Streptomyces longisporus ruber. *Landbauforschung Völkenrode* 11 (Nr. 3): 61–62.
Kullmann, A. [1958]. Über die Verrottung von Futterpflanzenwurzeln an Hand von Modellversuchen. *Z. Pfl.-Ernähr. Düng. Bodenk.* 84: 127–132.
Kurotori, T., and H. Matsumoto [1958]. Microscopical study of forest soils. I. On the method of making thin sections of soils for microscopic observation and the application of this technique to the study of forest soils. *Forest Soils of Japan, Report* 9.
Langton, J. E., and G. B. Lee [1965]. Preparation of thin sections from moist organic soil materials. *Proc. Soil Sci. Soc. Am.* 29: 221–223.
De Leenheer, L. [1967]. Variation in time of the soil porosity and pore size distribution—(general picture of a six-years study on a loamy soil). *Pedologie* 17: 341–374.
Lehmann, H., B. Meyer, and H. J. Schonlau [1969]. Die divergierende Humus-Metabolik benachbarter Sauer-Braunerden und Rendzinen unter Wald im Licht standortsbiologischer Untersuchungen. *Göttinger Bodenkundl. Ber.* 9: 1–63.
Lehner, A., and W. Nowak [1959]. Neuere Ergebnisse des Direktnachweises von Bakterien im Boden mittels der kombinierten Aufwuchs-Fluorochromierungsmethode. *Zentbl. Bakt. Parasitkde.,* 2nd Abt. 113: 32–34. 10/12.
Liese, W. [1964]. Uber den Abbau verholzter Zellwände durch Moderfäulepilze. *Holz als Roh- und Werkstoff* 22: 289–295.
———, and R. Schmid [1962]. Elektronenmikroskopische Untersuchungen über den Abbau des Holzes durch Pilze. *Angewandte Botanik* 36: 291–298.
Lieth, H., editor [1962]. *Die Stoffproduktion der Pflanzendecke.* Intern. Okol. Symp. Stuttgart-Hohenheim, Mai 1960. Stuttgart: Fischer.
Lindeberg, G. [1955]. Ligninabbau und Phenoloxydase-Bildung der Boden-Hymenomyceten. *Z. Pfl.-Ernähr. Düng. Bodenk.* 69: 142–150.
Linsbauer, K. [from 1922]. *Handbuch der Pflanzenanatomie.* 10 Vol. Berlin: Borntraeger.
Lohwag, H. [1941]. Anatomie der Asco- und Basidiomyceten. In Linsbauer [from 1922]. *Handbuch der Pflanzenanatomie.* Vol. 4.

Lund, Z. F., and H. O. Beals [1965]. A technique for making thin sections of soil with roots in place. *Proc. Soil Sci. Soc. Am.* 29: 633–635.

McKeague, J. A. [1971]. Organic matter in particle size and specific gravity fractions of some A_h-horizons. *Can. J. Soil. Sci.* 51: 499–505.

Mcmillan, J. H., and J. N. Healey [1971]. A quantitative technique of the analysis of the gut contents of Collembola. *Rev. Ecol. Biol. Sol* 8: 295–300.

Macfadyen, A. [1963]. The contribution of the microflora to total soil metabolism. In Doeksen and van der Drift, eds. *Soil Organisms*. Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

Mackenzie, A. F., and J. E. Dawson [1961]. The preparation and study of thin sections of wet organic soil materials. *J. Soil. Sci.* 12: 142–144.

Mader, D. L. [1953]. Physical and chemical characteristics of the major types of forest humus found in the United States and Canada. *Proc. Soil Sci. Soc. Am.* 17: 155–158.

Mader, H. [1958a]. Cutin. In Ruhland (Herausgeber): *Handbuch der Pflanzenphysiologie*. Vol. 10. Berlin, Göttingen, Heidelberg: Springer.

———. [1958b]. Kork. In Ruhland (Herausgeber): *Handbuch der Pflanzenphysiologie*. Vol. 10 Berlin, Göttingen, Heidelberg: Springer.

Maiwald, K. [1939]. Beschaffenheit des organischen Bodenanteils. In E. Blanck, ed. *Handbuch der Bodenlehre* Ergänzungs-Vol. 1. Berlin: Springer.

Malan, O. [1962]. Die Entwicklung der optischen Methoden zur Beurteilung von Braunkohlen. *Freiburger Forschungsheft A* 253: 5–21.

Martin, J. P., and K. Haider [1971]. Microbial activity in relation to soil humus formation. *Soil Sci.* 111: 54–63.

Meier, H. [1955]. Über den Zellwandabbau durch Holzvermorschungspilze und die submikroskopische Struktur von Fichten-Tracheiden und Birken-Holzfasern. *Holz als Roh- und Werkstoff* 13: 323–338.

Melhuish, F. M. [1968]. A precise technique for measurement of roots and root distribution in soils. *Ann. Bot.* 32: 15–22.

Menge, L. [1965]. Untersuchungen über das Gefüge und die Wasserbindungsintensität einiger Anmoor- und Moorböden. Diss., Landw. Hochschule Stuttgart-Hohenheim.

Metcalfe, C. R. [1960]. *Anatomy of the Monocotyledones*. I. Gramineae. Oxford: Clarendon Press.

———, and L. Chalk [1950]. *Anatomy of Dicotyledones*. 2 vol. Oxford: Clarendon Press.

Meyer, B., and E. Kalk [1964]. Verwitterungs-Mikromorphologie der Mineral-Spezies in mitteleuropäischen Holozän-Boden aus pleistozänen und holøzänen Lockersedimenten. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

Meyer, F. H. [1960]. Vergleich des mikrobiellen Abbaus von Fichten- und Buchen-Streu auf verschiedenen Bodentypen. *Archiv. Mikrobiologie* 35: 340–360.

———. [1962]. Vergleichende Mikrobiologie und Mikromorphologie der Humusbildung eines Buchen- und eines Fichten-Bestandes auf Basaltbraunerde. *Z. Pfl.-Ernähr. Düng. Bodenk.* 97: 234–243.

———. [1964]. The role of the fungus *Cenococcum graniforme* (Sow. Ferd. et Winge in the formation) of mor. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem, Amsterdam: Elsevier.

———. [1967]. Feinwurzelverteilung von Waldbäumen in Abhängigkeit vom Substrat. *Forstarchiv* 38: 286–290.

———. [1970]. Abbau von Pilzmyzel im Boden. *Z. Pfl. Ernahr. Dung. Bodenk.* 127: 193–199.

Michel, K. [1962]. *Mikrofotografie*. 2. Aufl., Wien: Springer.

Mikola, P. [1956]. Studies on the decomposition of forest litter by Basidiomycetes. *Comm. Inst. For. Fenn.* 48.2.

Minderman, G. [1956]. The preparation of microtome sections of unaltered soil for the study of soil organisms in situ. *Plant Soil* 8: 42–48.

Molisch, H. [1921]. *Mikrochemie der Pflanze*. 2. Aufl., Jena: Fischer.

Morozowa, T. D. [1963]. Micromorphological investigation of fossil soils. *Pochvovedenie* 9: 49–56.
Mückenhausen, E. [1962]. *Entstehung, Eigenschaften und Systematik der Boden der Bundesrepublik Deutschland.* 60 Tafeln, Frankfurt/Main: DLG-Verlag.
Müller, G. [1965]. *Bodenbiologie.* Jena: Fischer.
Müller, P. E. [1887]. *Studien über die natürlichen Humusformen.* Berlin: Springer.
Müllerstaël, H. [1962]. Humusbeschaffenheit und Pilzvegetation in einigen Buchen-und Fichten-Forsten des nordwestdeutschen Altdiluviums. Diss., Hamburg.
Müller-Stoll, W. [1936]. Untersuchungen urgeschichtlicher Holzreste nebst Anleitung zu ihrer Bestimmung. *Prähist. Z.* 27: 3–57.
———, [1951]. Mikroskopie des zersetzten und fossilierten Holzes. In Freund [from 1951]. *Handbuch der Mikroskopie in der Technik.* 8 Bände, Frankfurt/Main: Umschau-Verlag. Band 5.
Neuer, H. [1966]. Mengenanalyse mit dem Mikroskop. *Zeiss-Informationen* 60: 65–69.
Nicholas, D. P., and D. Parkinson [1967]. A comparison of methods for assessing the amount of fungal mycelium in soil samples. *Pedobiologia* 7: 23–41.
Nykvist, N. [1963]. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecica Nr. 3.*
Okafor, N. [1966]. The ecology of microorganisms on, and the decomposition of, insect wings in the soil. *Plant Soil* 25: 211–237.
Orlov, A. J. [1968]. Development and life duration of the pine feeding roots. Intern. Symp. USSR. USSR Acad. Sci., Leningrad: Nauka.
Oster, G., and A. W. Pollister [1955–1956]. *Physical Techniques in Biological Research.* New York: Academic Press.
Parfenova, Y. J., and Y. A. Yarilova [1960]. The problem of lessivage and podzolization. *Pochvovedenie* 9: 1–15.
————————. [1967]. Humus microforms in the soils of the U.S.S.R. *Geoderma* 1: 197–207.
————————. [1969]. Classification of soil fabric components. Third Intern. Working Meeting Soil Micromorphology, Wroclaw, Poland, Sept. 1969. Warszawa [1972]: Polska Akademia Nauk.
Parle, J. N. [1963]. Microorganisms in the interior of earthworms. *J. Gen. Microbiol.* 31: 1–11.
Pauli, F. W. [1958]. Fluorochrome Adsorption Studies on Decomposing Plant Residues. Diss., Potchefstroom.
———. [1960]. The fluorescence microscope in humus research. *Mikroskopie.* 15: 139–142.
———. [1961]. Flurochrome adsorption studies on decomposing plant residues. I. Decomposition studies. *South Afr. J. Agric. Sci.* 4: 123–134.
———, and J. H. Grobler [1961]. Characterisation of soil humus by acriflavine adsorption. *South Afr. J. Agr. Sci.* 4: 157–169.
von Pechmann, H. [1951] Die Mikroskopie in der Holzverarbeitungstechnik. In Freund (from 1951). *Handbuch der Mikroskopie in der Technik.* 8 Bände, Frankfurt/Main. Umschau-Verlag. Band 5.
Pettapiece, W. W., and M. A. Zwarich [1970]. Micropedological study of a chernozemic to grey wooded sequence of soils in Manitoba. *J. Soil Sci.* 21: 138–145.
Pinck, L. A., and F. E. Allison [1944]. The synthesis of lignin-like complexes by fungi. *Soil Sci.* 57: 155–161.
Ponomareva, S. J. [1962]. Die Bedeutung der biologischen Faktoren für die Steigerung der Fruchtbarkeit rasenpodsoliger Böden. *Z. Pfl.-Ernähr. Düng. Bodenk.* 97: 205–215.
von Post, H. [1862]. Studier öfver Nutidens koprogena Jordbildningar, Gyttja, Dy, Torf och Mylla. *Kgl. Svenska Vet.-Akad. Handl.*, N.F. 4, 1–59.
Prévot, A. R., M. Raynaud, G. Fischer, and B. Bizzini [1954]. Recherches sur la ligninolyse bacterienne dans le sol. Trans. 5ème Congrès International de la Science du Sol, Léopoldville 3:13.
Price, G. R., and S. Schwartz [1956]. Fluorescence microscopy. In Oster and Pollister, eds. *Physical Techniques in Biological Research.* Vol. 3. New York: Academic Press.
Puffe, D. [1965]. Gefügeuntersuchungen an Torfen. *Z. Kulturtechnik Flurbereinigung* 6: 301–312.
———, and G. Grosse-Brauckmann [1963]. Mikromorphologische Untersuchungen an Torfen. *Z. Kulturtechnik Flurbereinigung* 4: 159–188.

Radforth, N. W., and H. R. Eydt [1958]. Botanical derivatives contributing to the structure of major peat types. *Can. J. Bot.* 36: 153–163.

Righi, D. [1969]. Aspects morphologiques et physico-chimiques de la podzolisation en forêt de Rambouillet. Thèse de Doctorat 3ème cycle en Ecologie Végétale, 116p., Grignon.

Rinne, F., and M. Berek [1953]. *Anleitung zur optischen Untersuchung mit dem Polarisations mikroskop*· 2. Aufl. Stuttgart: Schweizerbart.

Rommell, L. G. [1935]. Ecological problems of the humus layer in the forest. Cornell-Univ. Agric. Exp. Sta. Memoir 170:2–28.

Rossi, G. [1936]. Direct microscopic and bacteriological examination of the soil. *Soil Sci.* 41: 53–66.

———, and G. Gesuè. Di un nuovo indirizzo nello studio biologico del suolo. *Ann. Technica Agr.* 3.

Roulet, N., P. Dubach, N. C. Mehta, M. Müller-Vonmoos, and H. Deuel [1963]. Verteilung der organischen Substanz und der Kohlenhydrate bei der Gewinnung "wurzelfreien" Bodenmaterials durch Schlämmsiebung. *Z. Pfl.-Ernähr. Düng. Bodenk.* 101: 210–214.

Ruch, F. [1956]. Birefringence and dichroism of cells and tissues. In Oster and Pollister, eds. *Physical Techniques in Biological Research.* Vol. 3. New York: Academic Press.

———.[1960]. Ein Mikrospektrograph für Absorptionsmessung im ultravioletten Licht. Z. *wiss Mikr.* 64:453–468.

———, and H. Hengartner [1960]. Quantitative Bestimmung der Ligninverteilung in der pflanzlichen Zellwand. Beih. z. d. Zeitschr. des Schweizerischen Forstvereins Nr. 30 (Festschrift Frey-Wyssling).

Ruttner, F. (1962). *Grundriss der Limnologie.* 3. Aufl. Berlin: de Gruyter.

Rypacek, V. [1960]. Die Veränderungen in der Struktur der verholzten Zellwand im Verlaufe der Humifikation (Czech, German summary). *Acta Agrobotanica* 9: 53–61.

———, [1966]. *Biologie der holzzerstörenden Pilze.* 2. Ausgabe. Jena: VEB G. Fischer.

Schaede, R. [1962]. *Die pflanzlichen Symbiose.* 3. Aufl. (neubearbeitet von F. H. Meyer), Stuttgart: Fischer.

Schaller, F. [1950]. Biologische Beobachtungen an humusbildenden Bodentieren, insbesondere an Collembolen. *Zool. Jb.* (*Syst.*) 78: 506–525.

Scheffer, F., and B. Ulrich [1960]. *Lehrbuch der Agrikulturchemie und Bodenkunde.* 3. Teü: *Humus und Humusdüngung.* Band I: Morphologie, Biologie, Chemie und Dynamik des Humus. 2. völlig neu bearbeitete Aufl. Stuttgart: Enke.

Schlenker, G. [1962]. Ertragspotentiale verschiedener Waldgesellschaften Südwestdeutschlands. In Lieth, ed. *Die Stoffproduktion der Pflanzendecke.* Intern. Okol, Symp. Stuttgart-Hohenheim, Mai 1960.

Schmid, R., and W. Liese [1964]. Über die mikromorphologischen Veränderungen der Zellwandstrukturen von Buchen- und Fichten-Holz beim Abbau durch Polyporus versicolor *From. Arch. Mikrobiol.* 47: 260–276.

Schroder, D. [1952]. *Unterscheidungsmerkmale der Wurzeln einiger Moor und Grünlandpflanzen nebst einem Schlüssel zu ihrer Bestimmung und einem Anhang für die Bestimmung einiger Rhizome.* Bremen: Schünemann.

Schuster, R. [1956]. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. *Z. Morph. Ökol. Tiere* 45: 1–33.

Sekera, F. [1956]. Beobachtungen über die Humusneubidung im Boden. *Phosphorsäure* 16 (Folge 3/4) 188–199.

———, and A. Brunner [1943]. Beiträge zur Methodik der Gareforschung. *Bodenkunde und Pflanzenernährung* 29 (74), 169–212.

Slager, S. [1964]. A study of the distribution of biopores in some sandy soils in the Netherlands. In A. Jongerius, ed. *Soil Micromorphology.* Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

Smolikova, L., and V. Lozek [1969]. Mikromorphologie und Molluskenfauna des mittelpleistozänen Aubodenkomplexes von Brozany (NW-Böhmen]. *Vestnik Ustredniho ustavu geologickeho* 44: 107–114.

Solar, F.[1960]. Zur Kenntnis der Böden auf dem Raxplateau. Diss., Hochschule für Bodenkultur, Wien.

Sørensen, H. [1962]. Decomposition of lignin by soil bacteria and complex formation between autoxidized lignin and organic nitrogen compounds. *J. Gen. Microbiol.* 27, 21–34.

Stamm, J. [1958]. Über das Vorkommen eosinophiler Zellschichten bei der Wurzel-Suberogenese einiger Pflanzen. *Photogr. und Wissenschaft* 2: 25–26.

Stephan, S. [1969]. Gefriertrocknung und andere bei der Herstellung von Bodendunnschliffen benutzbare Trocknungsverfahren. *Z. Pfl.-Ernähr. Dung. Bodenk.* 123: 131–140.

Stöckli, A. [1952]. Über den Abbau von Lignin, Zellulose und Hemizellulose durch Pilze–Versuche mit Streuematerialien, Holz und Ligninsulfonsäuren. Diss., E. T. H. Zürich.

Strugger, S. [1949]. *Fluoreszenzmikroskopie und Mikrobiologie.* Hannover: Schaper.

Szabo, J., M. Marton, and G. Partai [1964]. Micro-milieu studies in the A-horizon of a mull-like rendzina. In A. Jongerius, ed. *Soil Micromorphology.* Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———, M. Marton, L. Varga, and S. Schönfeld [1962]. Complex soil biological investigations of rendzina soils. *Pochvovedenie* 10: 85–95.

———, T. Bartfay, and M. Marton [1967]. The role and importance of the larvae of St. Mark's fly in the formation of a rendzina soil. In Graff and Satchell, eds. *Progress in Soil Biology.* Proc. Coll. Dynamics Soil Communities, 1966. Braunschweig: Vieweg.

Thoenes, W. [1960]. Giemsa-Färbung an Geweben nach Einbettung in Polyester ("Vestopal") und Methacrylat. *Z. wiss. Mikr.* 64: 406–413.

Thompson, S. O., G. Chesters, and L. E. Engelbert [1964]. Comparative properties of plant lignins and humic materials of soils. 1. Yields and cation exchange properties of plant lignins isolated by different techniques. *Proc. Soil Sci. Soc. Am.* 28: 65–68.

Tribe, H. T. [1963]. The microbial component of humus. In Doeksen and van der Drift, eds. *Soil Organisms.* Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

Trolldenier, G. [1965a]. Fluoreszenzmikroskopie in der Rhizosphärenforschung. *Zeiss-Informationen* 56: 68–69.

———. [1965b]. Fluoreszenzmikroskopische Untersuchung von Mikroorganismenreinkulturen in der Rhizosphäre. *Zentbl. Bakt. Parasitkde.*, 2. Abt. 119: 256–258.

Uggla, H., Z. Róg, and T. Woclawek [1969]. Micromorphology of the gyttja-muck soil of Jawty Male. Third Intern. Working Meeting Soil Micromorphology, Wroclaw, Poland, 1969. Warszawa [1972]: Polska Akademia Nauk.

Waksman, S. A. [1936]. *Humus.* Baltimore: Williams and Wilkins.

Welten, M. [1958]. Pollenanalytische Untersuchung alpiner Bodenprofile: historische Entwicklung des Bodens und säkulare Sukzession der örtlichen Pflanzengesellschaften. *Veröff. Geobot. Inst. Rübel*, H. 33, 253–274.

Wenzel, G., K. Kreutzer, and M. Alcubilla [1970]. Beitrag zur Klärung des Zusammenhanges zwischen Standort und Pilzhemmstoffgehalt des Fichtenbastes. *Fortswiss. Cbl.* 89: 372–381.

Wieringa, K. T. [1955]. Der Abbau der Pektine; der erste Angriff der organischen Pflanzensubstanz. *Z. Pfl.-Ernähr. Düng. Bodenk.* 69: 150–155.

Wilde, S. A. [1958]. *Forest Soils.* New York: Ronald Press.

———. [1971]. Forest humus: Its classification on a genetic basis. *Soil Sci.* 111: 1–12.

Willerding, U. [1960]. Beiträge zur jungeren Geschichte der Flora und Vegetation der Flussauen. *Flora* 149: 435–476.

Williams, S. T., and D. Parkinson [1964]. Studies of fungi in a podzol. I. Nature and fluctuation of the fungus flora of the mineral horizons. *J. Soil Sci.* 15: 331–341.

Wittich, W. [1939]. Untersuchungen über den Verlauf der Streuzersetzung auf einem Boden mit Mullzustand. 1. *Forstarchiv* 15: 96–111.

———. [1943]. Untersuchungen über den Verlauf der Streuzersetzung auf einem Boden mit Mullzustand. 2. *Forstarchiv* 19: 1–18.

Zachariae, G. [1962]. Zur Methodik der Geländeuntersuchungen in der Bodenzoologie. *Z. Pfl.-Ernähr. Düng. Bodenk.* 97: 224–233.

———. [1963]. Was leisten Collembolen für den Waldhumus? In Doeksen and van der Drift, eds.

Soil Organisms. Proc. Coll. Soil Fauna, Soil Microflora and Their Relationships, Oosterbeek. Amsterdam: North Holland Publishing Company.

———. [1964]. Welche Bedeutung haben Enchytraeen im Waldboden. In A. Jongerius, ed. *Soil Micromorphology*. Proc. 2nd Intern. Working Meeting on Soil Micromorphology, Arnhem. Amsterdam: Elsevier.

———. [1965]. Spuren tierischer Tätigkeit im Boden des Buchenwaldes. Forstwiss. Forschungen (Beihefte zum forstlichen Zentralblatt), H. 20.

———. [1966]. Die Streuzersetzung im Kohlgartengebiet. In Graff and Satchell, eds. [1967]. *Progress in Soil Biology*. Colloquium Dynamics of Soil Communities, Braunschweig Sept. 1966. Braunschweig: Vieweg.

———. [1967]. Der Einsatz mikromorphologischer Methoden bei bodenzoologischen Arbeiten. *Geoderma*. 1: 175–196.

Zajonc, J. [1967]. Über die Saisondynamik der Humusbildung durch Regenwürmer in einem Buchenwald der Karpathen. In Graff and Satchell, eds. *Progress in Soil Biology*. Proc. Coll. Dynamics Soil Communities, 1966. Braunschewig: Vieweg.

von Zezschwitz, E. [1965]. Biologische Aktivität und Basengehalt des Bodens. *Mitt. der Deutschen Bodenkundl. Gesellschaft* 4: 281–286.

Ziechmann, W., and E. Przemeck [1964]. Untersuchungen über die physiologische Wirkung von synthetischen und natürlichen Huminstoffen auf das Wurzelwachstum und auf die Phosphataseaktivität im Wurzelmeristem. Festschrift für F. Scheffer. Inst. für Bodenkunde, Göttingen.

Zöttl, H. [1965]. Zur Entwicklung der Rendzinen in der subalpinen Stufe. 1. Profilmorphologie. 2. Chemisch-biologische Dynamik. *Z. Pfl.-Ernähr. Düng. Bodenk.* 110: 110–114, 115–126.

Zvjagincev, D. G. [1964]. Study of shapes and sizes of soil microorganisms with the fluorescence microscope. *Pocvovedenie* 3: 101–105.